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**Sub-optimal Choice in the Brushtail Possum (*Trichosurus  
Vulpeca*): The Effect of Terminal Link Duration on Choice**

A thesis

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of the requirements for the degree

of

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## **Abstract**

Sub-optimal choice procedures are commonly used to investigate an animal model of human gambling, and the numerous variables which can affect choice responding (Zentall, 2011). This procedure typically presents two alternatives, one which provides less overall reinforcement than the other. This study aimed to examine whether manipulating terminal link duration on both alternatives would have an effect on possums level of preference towards either alternative, and whether possums would attend to overall reinforcement probability, or discriminative stimuli. Overall, subjects responded optimally at all terminal link durations, regardless of position of the optimal alternative. Response latencies towards the non-preferred alternative were longer than those towards the preferred alternative. Response rates towards both stimuli on the discriminative alternative were similar, indicating that possums were not discriminating between these stimuli. This suggests that terminal link duration does not affect preference when it is altered on both alternatives. The results of this study along with other research in this area suggests that the variables that appear to have the strongest influence on sub-optimal choice are impulsivity and reinforcer deprivation levels, or motivating operations.

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**Sub-optimal choice in the Brushtail possum (*Trichosurus vulpeca*): The effect of terminal link duration on choice.**

*Sub-optimal choice and the rationale behind animal models of human gambling*

According to Zentall (2011) both primary (learning) and secondary (thought) processes have been found to occur in decision making - humans often try to rationalize their decisions. Using animals to study human gambling behaviour eliminates the influence of secondary processes and social influences, and focuses on the primary processes underlying choice (Zentall, 2011).

Studies involving animals allow investigation of pathological behaviours without encouraging these maladaptive and potentially harmful behaviours in humans. Addiction based behaviours, such as pathological gambling, consist of behaviour being controlled by maladaptive decisions rather than adaptive ones, despite aversive consequences (Alessi & Petry, 2007; Potenza, 2009).

Maladaptive gambling, or sub-optimal choice, is described by Zentall (2011) as choosing the lower pay-off option of two alternatives. The lower pay-off option: may produce a smaller magnitude of reinforcement; may provide a lower probability of reinforcement; and may present a less profitable delay to reinforcement relative to the amount of reinforcement, when compared to the optimal alternative. Sub-optimal choice experiments typically implement concurrent chains procedures, involving an initial link response option which results in one of two possible, generally fixed time, terminal link response options on forced choice trials, and both terminal link options on choice trials (Lalli & Mauro, 1995). In several sub-optimal choice studies, pigeons have been found to respond sub-optimally within procedures that provide different reinforcement probabilities, different magnitudes of reinforcement, and different delays to

reinforcement (Pattison, Laude & Zentall, 2013). Research has suggested that pigeons' ability to attend to overall probabilities of reinforcement, in the presence of a highly predictable, low pay off stimulus, is limited (Laude et al., 2014). Sub-optimal choice results in larger overall losses than wins, and even experience with this contingency does not decrease the frequency of choosing the sub-optimal alternative (Zentall & Stagner, 2011b). It has been proposed that animals may respond sub-optimally, because in nature, being in proximity of a low probability, high payoff alternative actually increases the probability of the payoff occurring (Zentall & Stagner, 2011b). Animals often develop an initial preference for the optimal alternative, however, this preference generally reverses following repeated exposure to the discriminative (signals reinforcement or absence of reinforcement) and non-discriminative (does not signal outcome) alternatives and stimuli, and their corresponding reinforcement contingencies (Laude, Stagner & Zentall, 2014).

Procedures in which both alternatives signal trial outcomes, reliably or unreliably, have also shown that animals tend to prefer the lesser overall rate of reinforcement. This has been attributed to variation in outcomes (one versus two terminal link stimuli) (Gipson, Allesandri, Miller, & Zentall, 2009). A reliable alternative is one which presents the same stimulus on every trial. This stimulus always signals reinforcement. An unreliable alternative presents two discriminative stimuli with 50% probability of each stimulus. One always signals reinforcement (S+), and one always signals the absence of reinforcement (S-) (Spetch, Belke, Barnet, Dunn & Pierce, 1990). Many studies have found that partial, or unreliable, reinforcement is preferred over reliable reinforcement. Mazur (1996) suggests that an underlying preference for less overall

reinforcement is not sufficient enough explanation for the choice behaviour observed in research thus far, as this effect only occurs with stimuli which signal presence or absence of reinforcement. This effect is removed when the presentation of the discriminative stimuli is delayed, and when neither alternative is discriminative. There have been numerous variables found to affect choice responding, and various theories which aim to explain the effects of these variables.

#### *Signalled versus unsignalled alternatives*

Signalled alternatives are those in which the stimuli are discriminative, and provide information about forthcoming reinforcement, or the absence of reinforcement. Unsignalled conditions are those in which the stimuli are non-discriminative, and provide no information about forthcoming reinforcement. Mazur (2005) states that when one or both alternatives are signalled or unsignalled, there are varying effects on choice responding. In conditions in which both alternatives are unsignalled, animals will prefer an alternative which provides a larger amount, or higher overall rate of reinforcement, however, in signalled conditions, the alternative providing less reinforcement is preferred (Mazur, 2005).

Although research conducted using pigeons has found preferences for the signalled alternative, investigation of choice responding in rats has revealed contrasting results. They prefer the alternative which provides less information about forthcoming reinforcement, even when reinforcement probabilities are equal on both alternatives. Petri (1974) exposed rats to one alternative that provided reinforcement on alternating trials (overall reinforcement rate of 50%) and another alternative which provided reinforcers randomly on 50% of trials. The rats had

longer latencies to non-reinforced trials on the alternating schedule suggesting that they were able to discriminate between the two alternatives, and the information provided by these alternatives regarding reinforcement. The rats showed no preference between schedules. When then given two alternatives with the same reinforcement contingencies (i.e. both alternating schedules, or both random schedules), one of which had a tone signalling reinforced trials, the rats preferred the alternative without the tone. Petri (1974) suggests that it may have been the increased predictability of non-reinforcement (absence of tone) that led to the rats' preference for the unsignalled alternative.

#### *Reliable versus unreliable alternatives*

Early research in the area of sub-optimal choice (Belke & Spetch, 1994; Kendall, 1974; Kendall, 1985; Pierce, 1990; Spetch et al., 1990) presented reliable and unreliable alternatives. When reliable and unreliable alternatives have been provided on concurrent chains schedules, a preference has been found for the unreliable alternative. Spetch et al. (1990) suggest that preference for the sub-optimal alternative results from the absence of reinforcement on 50% of trials on the unreliable alternative, which strengthens the conditioned association of the S+ and its consistent reinforcement. Similarly, Dunn and Spetch (1990) suggested that the stimulus on the reliable alternative does not serve as a conditioned reinforcer as it does not signal a reduction in delay to reinforcement - the delay is the same on every trial. However on the unreliable alternative, the stimulus associated with 50% reinforcement does signal a reduction in delay to reinforcement when compared to a trial where the S- is presented, which signals an increase in delay to reinforcement (due to reinforcement being withheld until the S+ is presented on a trial).

### *Magnitude of reinforcement*

A common procedure used to examine choice responding involves manipulating reinforcer magnitudes and probabilities associated with each stimulus. Generally, one alternative provides, on average, 2 pellets per trial (20% of trials are reinforced with 10 pellets, while the other 80% of trials go unreinforced) and the other alternative provides 3 pellets on every trial. Molet et al. (2012) used this procedure to examine choice in humans, and was therefore able to examine human behaviour within this procedure, rather than to extrapolate the results found with animals. Participants were assigned to groups (gambler or non-gambler) based on self-report. Those who considered themselves gamblers responded sub-optimally, and those who considered themselves to be non-gamblers responded optimally. However, on average, the self-reported gamblers responded almost indifferently (56.5% of choices towards the sub-optimal alternative). Molet et al. (2012) did however state that the non-gamblers choice percentage (23%) was used as a baseline, and therefore, the gamblers were much more sub-optimal than non-gamblers.

### *Optimal foraging theory*

Optimal foraging theory states that animals will choose to maximise the ratio of reinforcement to time spent working for, or searching for, reinforcement (Vasconcelos, Monteiro, & Kacelnik, 2015). In a natural setting, it is expected that animals will prefer a stimulus that is associated with a larger probability of reinforcement (Laude, Beckman, Daniels & Zentall, 2014).

Fantino and Abarca (1985) suggest that as the time spent foraging increases, animals' preference for the initially preferred alternative should decrease, and responding to the less preferred alternative should increase because

they become less selective, and begin to search for any food alternative rather than the more profitable one. In an operant setting, this equates to the effect that the time in the choice phase (from initial link response to terminal link response) has on preference. When the time in the choice phase (search) is longer than the terminal link (delay to food once food has been sighted), preference for the non-preferred alternative should increase. It is suggested that this preference should not be affected by whether the animal is performing in an open or closed economy (Fantino and Abarca, 1985). This is inconsistent with works by Baum (1982), Dunn (1982), Pliskoff, Cicerone and Nelson (1978) and Pliskoff and Fetterman (1981), who all found that as time in the choice phase increased, so too did initial preference

#### *Information theory*

Information theory can account for preference for discriminative stimuli associated with less reinforcement over non-discriminative stimuli associated with more reinforcement. It states that the most information is gained when the discriminative stimulus signals a large change in information about the likelihood of reinforcement (Zentall, 2011; Vasconcelos et al., 2015) For example a stimulus that signals 100% reinforcement on an alternative which provides 20% reinforcement overall should be preferred over an alternative with two stimuli which signal reinforcement on 50% of trials. Preference for the signalled alternative would therefore be strongest when the probability of reinforcement on that alternative is low because the S+ stimulus would produce large contrast, or reduction in uncertainty, when compared to higher reinforcement probabilities (Roper and Zentall, 1999).

#### *Food deprivation and social interaction levels*

Zentall (2015) proposes that choosing sub-optimally may in fact be adaptive in nature, and therefore optimal responding has not needed to occur. Although, in a choice between risky (sub-optimal) and non-risky (optimal) alternatives, it would be expected, due to natural selection and optimal foraging theory, that animals would prefer the non-risky option (Bateson, 2002). Whether an animal is risk sensitive or not is likely due to their state of food deprivation – animals tend to be risk averse when they are in an energy surplus, and risk prone when they are in an energy deficit. This is because in an energy surplus, average consumption is higher than starvation levels, and in an energy deficit, average consumption is below starvation levels. Lower variance in reinforcement therefore corresponds to a low probability of starvation when in an energy surplus, and higher variance in reinforcement corresponds to a high probability of survival when in an energy deficit (Bateson, 2002). Laude, Pattison and Zentall (2012) investigated whether a higher level of food deprivation, and therefore higher motivation, would cause pigeons to respond sub-optimally, and found that hungry pigeons responded sub-optimally, and less hungry pigeons responded optimally. This may also suggest that, experimentally, more hungry animals attend to discriminative stimuli, whereas less hungry animals attend to overall rate of reinforcement.

Pompilio and Kacelnik (2005) found that deprivation level in training has been found to affect choice when the animal is not deprived. They tested the hypothesis that subject's experience within the contingencies, rather than the overall rate or amount of reinforcement, affects responding. They found that the alternative in which the starlings were more deprived during training became the preferred alternative during testing, and that as the delay to reinforcement

increased, the preference for that alternative decreased, and subjects became indifferent when the preferred alternative had a delay of 17.5-s, while the delay to reinforcement on the non-preferred alternative remained constant at 10-s. These results suggest that the value that has been attributed to the alternatives in training carries through to testing, supporting the findings of previous research (Pompilio & Kacelnik, 2005).

Impulsivity can also potentially account for the differences observed in more and less deprived animals. The response times of the more deprived pigeons suggest that they were more impulsive, as they responded faster to the sub-optimal alternative on forced choice trials than to the optimal alternative on forced choice trials (Laude et al., 2012).

Social and environmental deprivation affects choice responding in a manner similar to food deprivation. Pattison et al. (2013) investigated the effects of environmental enrichment on sub-optimal choice using alternatives providing 50% and 75% overall reinforcement. They found that pigeons who were given social and environmental enrichment responded more slowly, and less often to the sub-optimal alternative, however they still responded sub-optimally overall. The enriched pigeons may have inhibited certain behaviours while in contact with other pigeons in the shared environment, and that this inhibition may have generalised to their impulsive behaviour of responding to the sub-optimal alternative (Pattison et al., 2013).

#### *Discriminative stimuli and conditioned reinforcers*

Conditioned reinforcement is the factor most commonly attributed to sub-optimal responding (Roper & Zentall, 1999). Stimuli become conditioned reinforcers when they predict reinforcement. Stimuli associated with a higher rate

of reinforcement (e.g. 100%) are better conditioned reinforcers than those associated with a lower rate of reinforcement (e.g. 50%), even when the stimuli with higher reinforcement rates are paired with a stimulus which always signals non-reinforcement (S-) (Zentall & Stagner, 2015). Animals that respond sub-optimally are attending to the reinforcement probabilities of the discriminative stimuli, rather than the overall rate of reinforcement on both alternatives (Laude et al., 2014a). This discriminative stimulus, also called the S+ has then become a conditioned reinforcer.

Stagner, Laude, and Zentall (2012) hypothesised that pigeons will attend to the S+ and ignore the S- when the S+ for that alternative reliably predicts reinforcement. The effect that an S+ has on choice diminishes when the S+ predicts reinforcement less reliably. This can account for an observed preference of an S+ which occurs 50% of the time and provides reinforcement 100% of the time, over two stimuli which both occur 50% of the time and predict reinforcement 75% of the time. Although the first alternative provides less overall reinforcement, the S+ is a stronger conditioned reinforcer than the two stimuli on the alternative that provides more reinforcement overall (Stagner et al., 2012). Similarly, Stagner and Zentall (2010) found that pigeons preferred 20% overall reinforcement over 50% overall reinforcement as the stimulus providing reinforcement on the sub-optimal alternative was a stronger conditioned reinforcer than both stimuli on the optimal alternative.

Observing responses (responses that produce discriminative stimuli) have been researched in humans and non-human animals, and it has been found that they will perform observing responses, often with large response requirements, suggesting that discriminative stimuli are preferred due to the strength of these

stimuli as conditioned reinforcers (Lalli & Mauro, 1995). As sub-optimal alternatives generally offer less frequent (and more reliable) conditioned stimuli than sub-optimal alternatives, Laude et al. (2014b) suggest that it is the value of the conditioned reinforcer rather than the frequency that it occurs which controls responding.

Alternatively, Zentall and Stagner (2011b) suggest that it is not the value of the conditioned reinforcer that influences responding, but the reduction in uncertainty of reinforcement that follows presentation of the discriminative stimuli. A response on the non-discriminative alternative is followed by an unreliable stimulus, and reinforcement is still uncertain until the end of the terminal link. Responding on the discriminative alternative, however, immediately provides a stimulus which indicates whether or not reinforcement will be provided (Zentall & Stagner, 2011b).

#### *Absence of conditioned inhibition*

As S+ stimuli result in conditioned reinforcement, S- stimuli should theoretically result in conditioned inhibition (a decrease in responding, or increased response latency to the stimulus which predicts reliable non-reinforcement). Research in this area has so far failed to consistently observe this phenomenon (Stagner, Laude & Zentall, 2011). Sequential theory provides a possible explanation for decreased inhibition towards the sub-optimal alternative as it states that when reinforcement occurs, it reinforces the behaviour on any non-reinforced trials that occur between reinforced trials (Laude et al., 2014b). The preference reversal from the initial optimal preference to a sub-optimal preference following experience with the alternatives has been attributed to the decreased inhibitory effect of the S-. Repeated exposure to the S- reduces the negative effect

of non-reinforcement (Laude et al., 2014b). Preference for conditioned reinforcers can differ across levels of impulsivity – higher impulsivity leads to preference for conditioned reinforcers. This may also be related to conditioned inhibition.

Animals with a smaller preference for the sub-optimal alternative, or a preference for the optimal alternative, may be attending more to the S- than those with a larger preference (Laude et al., 2014a).

#### *Positive contrast and within trial contrast*

Lalli and Mauro (1995) explain preference for high probability alternatives in unsignalled and low probability alternatives in signalled conditions by suggesting that a stimulus functions as a stronger reinforcer when non-reinforcement also occurs in the same context. This is also referred to as positive contrast – an alternative that always provides reinforcement has no positive contrast as reinforcement is always expected, whereas an alternative that provides reinforcement on 50% of trials has larger positive contrast between reinforcement (100%) and the initial unreliable probability of reinforcement (50%). Roper and Zentall (1999) designed an experiment to test this hypothesis in which they found a preference for the discriminative stimuli when the overall rate of reinforcement was high (87.5%), however the preference for the discriminative alternative was stronger when the overall probability of reinforcement was low (12.5%), as there was more positive contrast at the low probability when compared to the high probability. Value enhancement hypothesis supports the idea of positive contrast as it predicts that exposure to an S- increases the conditioned value of the S+ (Belke and Spetch, 1994).

Animals have been found to prefer an alternative with a larger response requirement than one with a smaller response requirement because time spent

responding with a larger requirement equates to a smaller portion of total trial time. This is referred to as within trial contrast (Pompilio & Kacelnik, 2005). Similarly, in terms of delay reduction, Singer and Zentall (2011) proposed that when terminal link durations are equal for high and low workload alternatives, the high workload alternative should be preferred, as the terminal link as a proportion of the total trial duration, from initial link to outcome, is less in the higher workload alternative. The value of a discriminative stimulus is increased when response requirements are higher, food deprivation is higher, delay to reinforcement is longer, and the absence of reinforcement occurs, compared to another discriminative stimulus which provides the same reinforcer, but has less response requirements, lower food deprivation, shorter delays, and is followed by reinforcement. Within trial contrast is analogous to justification of effort in humans. Similarly, Blaszczynski and Nower (2002) proposed that behavioural persistence may account for the continuation of behaviour which often results in negative consequences, which may provide an explanation for problem gambling behaviour.

*Delay reduction and the extension of this model to probability of reinforcement*

Delay reduction hypothesis states that a stimulus becomes a stronger conditioned reinforcer if it signals a reduced time to reinforcement (Fantino & Abarca, 1985; Roper & Zentall, 1999). Spetch and Dunn (1987) manipulated the terminal link duration of both alternatives in a choice procedure, and found that as the terminal link duration increased, preference for the optimal alternative increased. The delay reduction hypothesis can also be extended to reinforcer magnitudes in that larger magnitudes should be preferred over smaller magnitudes when delay to reinforcement is the same. Zentall and Stagner (2011b) investigated

whether pigeons were choosing the sub-optimal alternative to avoid the more uncertain stimulus probabilities, or whether they preferred the information provided by discriminative stimuli. They used the typical magnitude procedure and found that most pigeons preferred the sub-optimal alternative, and all pigeons chose optimally when the probability and magnitude of reinforcement was equated. This suggests that pigeons' choice was influenced by discriminative stimuli, rather than variability in reinforcement.

This can also be extended to reinforcement probabilities – a larger reinforcement probability should be preferred over a smaller reinforcement probability when time to reinforcement is reduced (Spetch & Dunn, 1987). Extending the delay reduction hypothesis to reinforcement probabilities could be used to mimic probabilistic situations that animals would encounter in the wild.

#### *Delay discounting/impulsivity*

Delay discounting refers to the degree to which reward value changes dependent upon its delay to presentation. Potenza (2009) states that steeper delay discounting occurs in those with addictions compared to those without, and as impulsivity has been found to be a risk factor in addictive behaviours, those who discount delays more steeply are likely to be more impulsive. This is supported by much of the literature in which animals who are categorised as “impulsive” prefer the sub-optimal alternative, and in humans, those who labelled themselves gamblers, responded sub-optimally when compared to those who labelled themselves non-gamblers (Potenza, 2009). Further supporting this claim, Laude et al. (2014a) found that degree of discounting was positively correlated with sub-optimal preference - pigeons who discounted delayed reinforcers more steeply (were more impulsive) acquired a sub-optimal preference faster than the pigeons

who discounted less steeply (less impulsive).

Pattison et al. (2013) found that pigeons who were socially enriched, and therefore responded optimally, had longer response latencies than those who were socially deprived. They suggested that this may have occurred due to pigeons inhibiting certain behaviours while in the presence of other pigeons. Behavioural inhibition may have generalised to key pecking behaviour, and as a result, their responding became less impulsive, and more self-controlled (Pattison et al., 2013).

Molet et al. (2012) investigated the effects of depleted self-regulatory abilities on impulsive choice. They found that those whose self-regulation was depleted responded sub-optimally, as the self-reported gamblers did (55%) and those in the control group responded optimally (38%), however less optimally than the non-gamblers.

#### *Inter-trial intervals (ITI)*

Mazur (2007) reports previous research with conflicting findings between rats and pigeons – discriminative stimuli tend to be preferred by pigeons, and therefore, their indifference points occur at much larger ITIs when reinforcement is signalled than when it is unsignalled (Mazur, 1989). It was suggested that this preference occurred because time spent in the presence of a discriminative stimulus and the frequency of reinforcement in the presence of the stimulus affects its strength as a conditioned reinforcer, rather than the total amount of time from response to reinforcement. Contradictory findings have resulted from similar experiments with rats – ITI length appears to affect rats' choice. Responding towards the sub-optimal alternative decreased as the ITI duration was increased. Mazur (2007) suggests that this is because rats are less sensitive to discriminative stimuli than to time from response to reinforcer, and therefore overall

reinforcement rate as this is altered by changes in delay to reinforcement, including ITIs as the ITI duration alters the time from response to reinforcer when trials are not reinforced. The reason for this difference between species is unclear. Because ITI duration has been found to affect responding when altered, it was kept constant during this experiment.

#### *Manipulating terminal link duration*

Preference for the sub-optimal alternative has been found to be stronger at longer terminal link durations (Lalli & Mauro, 1995). Zentall and Stagner (2011a) used a forced choice procedure, and manipulated the terminal link duration of a non-discriminative alternative to investigate the terminal link duration at which pigeons would become indifferent between the preferred discriminative alternative and the non-discriminative alternative. They found that pigeons became indifferent when terminal link duration was approximately half that of the discriminative alternative, and that the optimal alternative became the preferred alternative when the terminal link duration was more than half that of the discriminative alternative. Mazur's (1989) hyperbolic decay model can account for this preference reversal as it states that reinforcers lose their value when the time between response and reinforcer is increased.

Spetch et al. (1990) investigated choice between signalled reliable (100%) and unsignalled, unreliable (50%) reinforcement alternatives in pigeons, and the effect of terminal link duration on preference for these alternatives. Their results were consistent with those of Zentall and Stagner (2011a) in that the sub-optimal alternative was preferred when terminal link durations were longer, and the optimal alternative was preferred when terminal link durations were short. When terminal link duration was increased, and time between outcomes and time in the

choice phase were equated, preference reduced. This suggests that terminal link duration is more important than both the time between reinforcers/blackouts, and the time in the choice phase in determining choice behaviour.

#### *Visual capabilities of the Brushtail possum*

Of the few studies investigating Brushtail possums' visual capabilities, most research focusses on the physiological aspects of sight, rather than using behavioural methods (Signal, 2002). Hill (2016) and Hancox (2016) implemented concurrent chains choice procedures in which possums were required to discriminate between horizontal, vertical and alternating diagonal lines and their corresponding reinforcement contingencies. They found that possums were able to discriminate between the reinforcement contingencies. A follow the light procedure using various visible colours was implemented by Vanstone (2006). All stimuli were reliably detected, apart from red. Although possums have difficulty distinguishing between mid to long wavelength colours, this does not mean that they cannot detect them (Thomas & Maddigan, 2004). The lack of detection observed by Vanstone (2006) likely occurred as a result of the red lighting in the experimental room. Thomas and Maddigan (2004) and Vlahos, Knott, Valter, and Hemmi (2014) suggested that because possums are nocturnal, it is likely that they have di-chromatic vision, and they therefore may have trouble distinguishing between middle to long wavelength colours – a trait common to animals which are active in the dark - although some recent research indicates that some marsupials may in fact have tri-chromatic vision. Based on the little research there is, peak visual sensitivity for Brushtail possums is thought to occur at 544nm (Vlahos et al., 2014). Given this probability that possums are unable to distinguish between mid to long wavelength colours and the fact that red light was already

present within the experimental area, red (a long wavelength colour) was eliminated as a possible stimulus.

Signal (2002) examined critical flicker fusion in the Brushtail possum, and determined that on average, the possums in her experiment had a threshold of approximately 20-25Hz, and that discrimination between flickering and still lights could be performed easily by possums when the flicker was set to 5Hz. With some indication of which colours possums should theoretically be able to discriminate, along with the results found by Signal (2002) regarding ability to discriminate between flickering and still lights, this experiment used blue (470nm) and yellow (593nm) still and flickering choice stimuli, with a blue-green stimulus (511nm) being used as the initial link and forced or choice trial indicator.

The purpose of this experiment was to use a concurrent chains procedure similar to Zentall and Stagner (2011a) to examine whether manipulating the terminal link duration on both discriminative and non-discriminative alternatives would result in a preference reversal, and also whether a reversal would occur regardless of which alternative was initially preferred i.e. sub-optimal to optimal, or optimal to sub-optimal. Zentall and Stagner (2011a) altered only the terminal link duration of the sub-optimal alternative, however, the current experiment altered the terminal link duration of both alternatives to examine preference across a range of equal delays. This procedure is therefore similar to those which present reliable and unreliable alternatives, as well as Zentall and Stagner's (2011b) procedure using different magnitudes of reinforcement with the same terminal link duration on both alternatives. This is because it will examine the effects of reinforcement probabilities at equal terminal link durations, while also observing any differences in within group responding at varying terminal link durations. A

preference for the sub-optimal alternative under these conditions would indicate that Brushtail possums choice responding is controlled by discriminative stimuli, and a preference for the optimal alternative would indicate that choice responding is controlled by overall reinforcement probabilities. Choice is considered sub-optimal when the alternative providing less overall reinforcement is selected on more than 50% of choice trials in a session. Consistent sub-optimal choice would show a preference for the sub-optimal alternative.

Based on Hill's (2016) and Hancox's (2016) research, it is hypothesised that possums will prefer the optimal alternative, suggesting that responding is controlled by overall reinforcement probabilities, rather than discriminative stimuli. If the optimal alternative is preferred, the possums are also expected to produce longer response latencies to the sub-optimal alternative than to the optimal alternative. When terminal link duration is decreased, response latencies to the less preferred alternative should also decrease. If the possums are attending to the stimuli, it is expected that response rate during the terminal link towards the S+ will be higher than the S-.

## Method

### *Subjects*

Six male Brushtail possums (*Trichosurus vulpecula*), aged 2 to 13 years, were used as subjects for this experiment. Table 1 shows the subject number, name, sex, and approximate age for each possum. A7, A8, A9, A11 and A12 had previous experimental experience (as listed in the attached ethics approval form). A10 was experimentally naïve and needed to be trained to press levers prior to the experiment.

All possums were maintained at a weight at which they were motivated to work. Target weights were achieved by giving each possum 140g of feed – dock and apple or carrot – and monitoring the amount of food consumed in the experimental sessions. Supplementary feed of pellets was then altered to maintain body weight which produced reliable responding across experimental sessions. Weight loss below that at which a possum reliably responded was countered by increasing supplemental pellets. Figure 1 shows the weights and feed amounts for each subject. Previous target weights were outdated and therefore discarded. This accounted for the large changes in weights and supplementary feed which can be seen in Figure 1.

All possums had constant access to water through a water nipple at the top of their cages. This experiment was approved by the University of Waikato Animal Ethics Committee (Protocol #956).

### *Apparatus*

The possums were housed in a laboratory room which was on a reverse 12:12 hour light/dark cycle. The room could be illuminated with three 60 watt red

Table 1.

*Subject number, name, sex, and approximate age of each subject.*

---

<b>Subject number</b>	<b>Name</b>	<b>Sex</b>	<b>Approximate age</b>
A7	Ishan	M	13
A8	Dexter	M	9
A9	Frank	M	8
A10	Kanji	M	2
A11	Riley	M	6
A12	Wilbur	M	12

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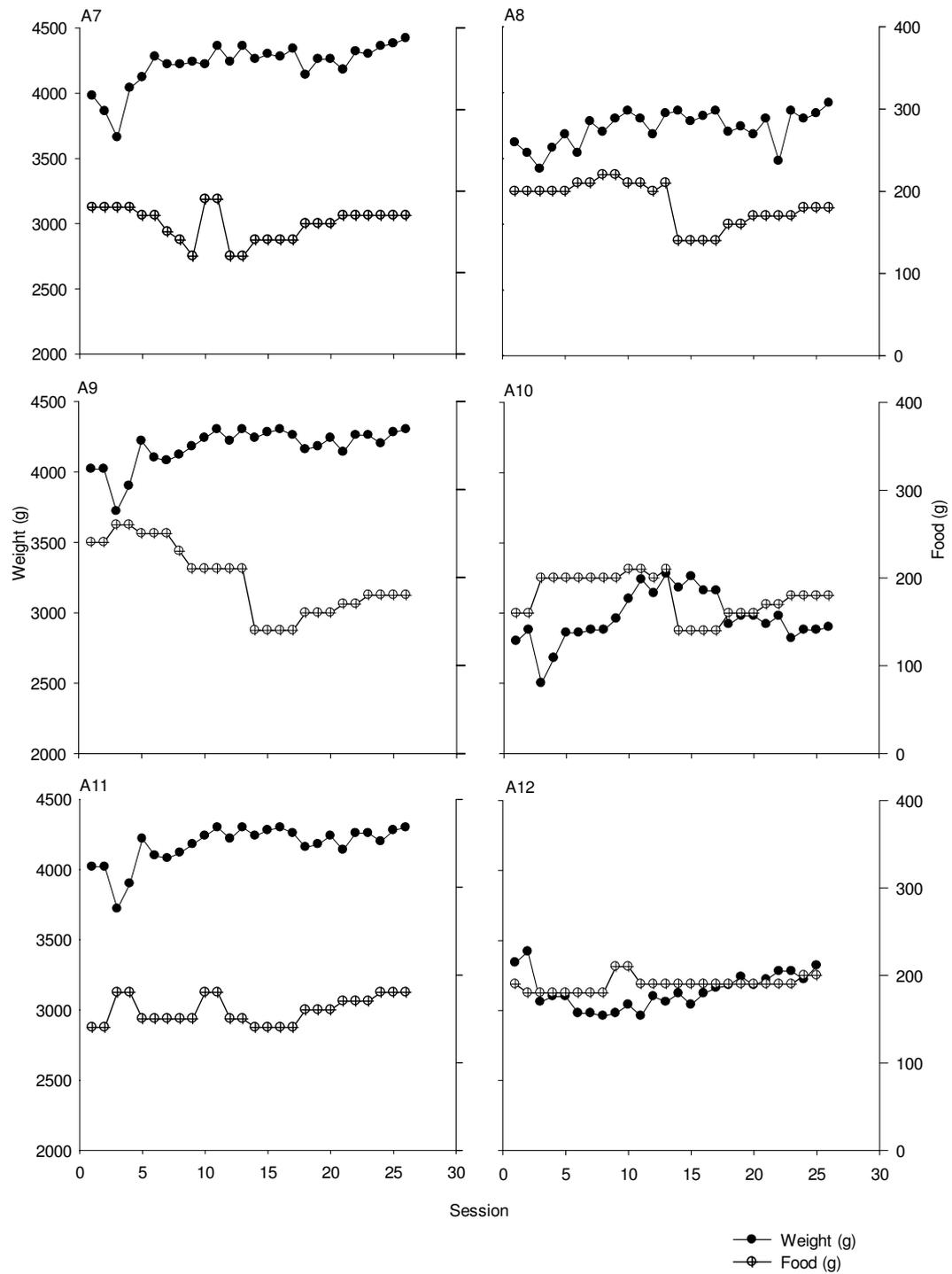


Figure 1. Weights and feed amounts for each possum across the experiment.

light bulbs during the dark cycle. These lights did not disturb the possums, but did allow visibility for the researchers during the dark cycle. Experiments were conducted in the possums' individual wire grid home cages (550mm x 1000mm x 580mm) with a shelf 250mm from the top of the cage. A wooden nesting box (450mm x 190-360mm x 300mm), with constant access, sat at the top of each cage. Metal shields were placed between each cage to block access to the neighbouring cages. These cages had a slot cut out for food trays immediately to the left of the hinged 300mm by 450mm response panel (Figure 2 and Figure 3), which sat 50mm from the base of the cage. The response panel, comprised of plywood backed with dark Perspex, and also functioned as the cage door. 3-s access to the reinforcer was delivered by a magazine which sat in a 100mm by 130mm cut out 100mm from the base of the response panel. When the magazine was raised, food could be accessed through a hole in the magazine approximately 30mm in diameter. Three levers were centred 50mm above the top of the magazine cut out, and were spaced 100mm apart. The base of the stimulus LED lights sat 5mm above each lever.

Experimental events for all sessions were controlled and recorded with Med-PC from a computer in a room adjacent to that which housed the possums. For a lever press to be recognised, 0.2N of force was required.

### *Procedure*

Experimental sessions were run during the dark cycle which began at approximately 9am every day, with the experiment beginning between 9am and 10.30am. Experimental sessions were terminated following 120 trials (40 left forced choice, 40 right forced choice, and 40 choice) or 7200-s, whichever occurred first. Each condition involved three levers.

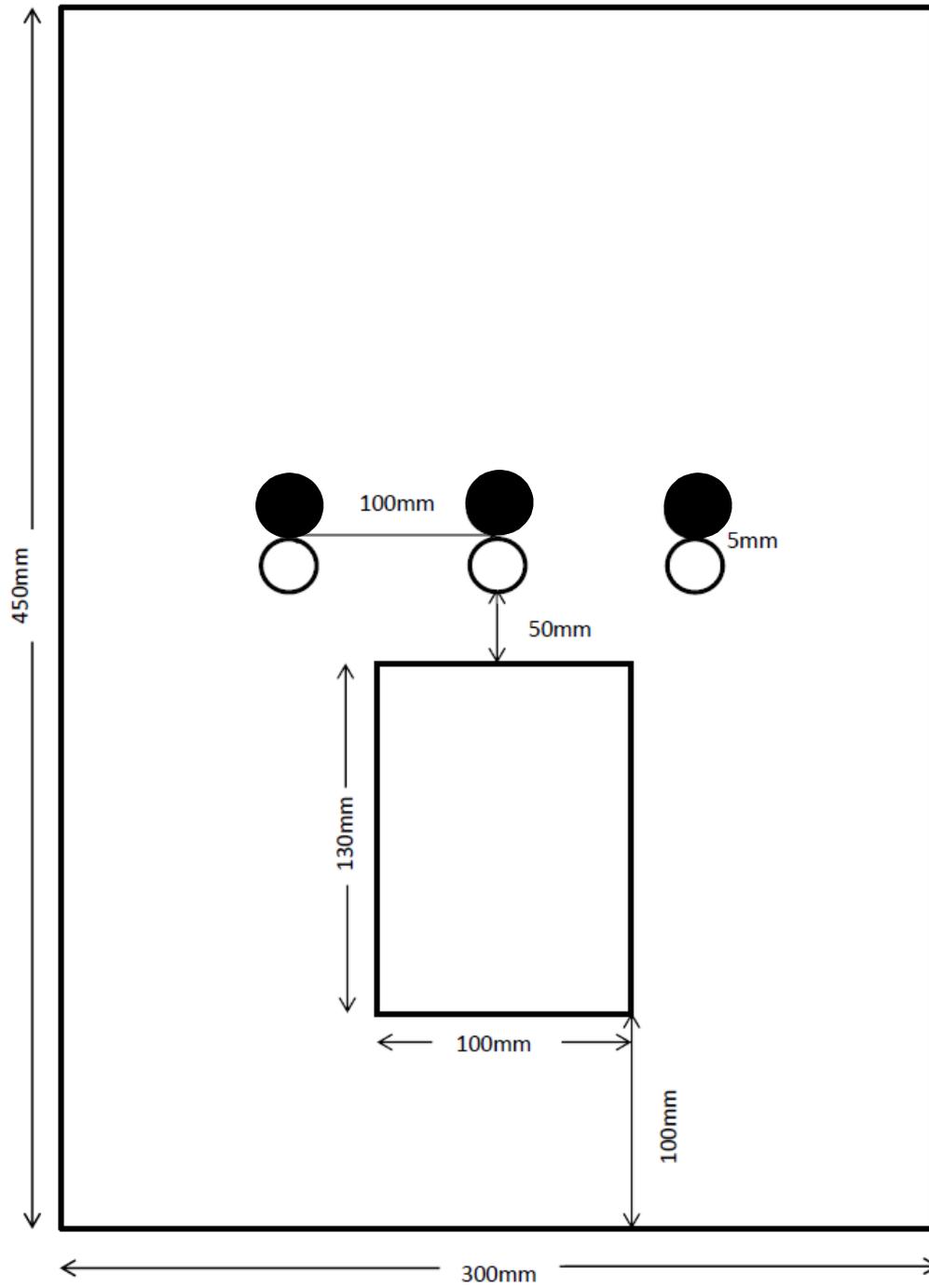


Figure 2. Diagram of response panel measurements.

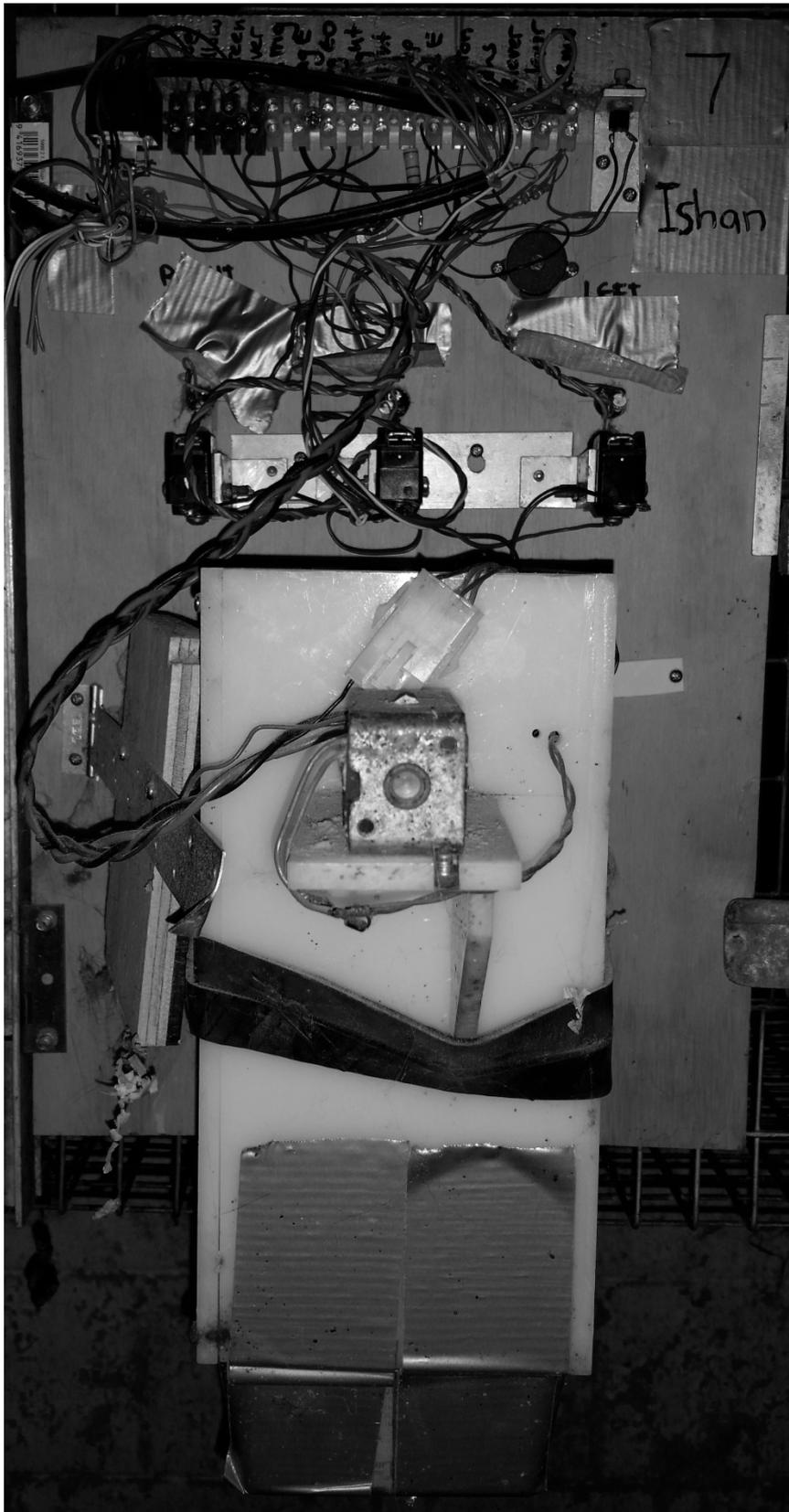


Figure 3. Response panel.

This experiment used a concurrent chains procedure. In all conditions, the central lever initiated either a forced choice or choice trial. Forced choice trials consisted of either only the left or right green-blue LED (511nm) being illuminated. In choice trials, both left and right green-blue LEDs were illuminated. Pressing an illuminated left or right lever initiated the terminal link in which a blue still, blue flickering (both 470nm), yellow still, or yellow flickering (both 593nm) light was presented. The flicker was set at 5Hz. In all conditions, a left lever press resulted in either a blue still or blue flickering light, and a right lever press resulted in either a yellow still or yellow flickering light. Terminal link duration was manipulated following at least six sessions in which the possums completed two or more choice trials. The experimental terminal link durations used in all three conditions were 10-s, 8-s, 6-s, and 4-s. During training in Condition 1, six sessions at 1-s, 2-s, 4-s, 6-s, 8-s and 10-s terminal link durations were used incrementally to gradually introduce the possums to the delays, and to ensure that they would work at these values. Following six training sessions of reliable responding at 10-s during Condition 1, experimental sessions with 10-s terminal link duration began. Following six sessions of reliable responding at each experimental terminal link duration, terminal link duration was reduced. On a reinforced trial, subjects received 3-s access to the reinforcer. Non-reinforced trials were followed by a 3-s blackout to prevent the overall rate of reinforcement being altered by ensuring the time between trials is the same. An inter-trial interval of 1s followed each trial, both reinforced and non-reinforced.

The lever side of each alternative, stimuli and their probabilities of presentations on both alternatives, and the reinforcement probabilities of each alternative are presented in Table 2.

Table 2. *Lever side, stimuli, stimulus presentation probability, and corresponding reinforcement probabilities of each stimulus for sub-optimal and optimal alternatives in each condition. Condition 1 did not have a sub-optimal alternative, as both alternatives were of equal probability, and were non-discriminative. Condition labels display the left alternative overall reinforcement rate and the right alternative overall reinforcement rate. 100%S+ / 0%S- and 50%S1 / 50% S2 show colours of the stimuli associated with the alternatives. PS + / S- and P S1 / S2 show the presentations probability of each stimulus. P(rft) S+ / S- and P(rft) S1 / S2 show the reinforcement probabilities of each stimulus.*

<b>Sub-optimal discriminative alternative</b>				
<b>Condition</b>	<b>Side lever</b>	<b>100% S+ / 0% S-</b>	<b>P S+ / S-</b>	<b>P(rft) S+ / S-</b>
2. .20 / .50	L	Blue flicker / blue still	0.2 / 0.8	1.0 / 0.0
3. .50 / .20	R	Yellow flicker / yellow still	0.2 / 0.8	1.0 / 0.0
<b>Optimal non-discriminative alternative</b>				
<b>Condition</b>	<b>Side lever</b>	<b>50% S1 / 50% S2</b>	<b>P S1 / S2</b>	<b>P(rft) S1 / S2</b>
1. .50 / .50	L/R	L-Blue flicker / blue still R – Yellow flicker / yellow still	0.5 / 0.5	0.5 / 0.5
2. .20 / .50	R	Yellow flicker / yellow still	0.5 / 0.5	0.5 / 0.5
3. .50 / .20	L	Blue flicker / blue still	0.5 / 0.5	0.5 / 0.5

### Condition 1:

In this condition, the probability of each stimulus as well as the probability of reinforcement was set at 50%. On the left lever, there was a 50% chance of a blue flickering light, and 50% chance of a blue still light, both of which provided reinforcement on 50% of presentations. On the right lever, there was a 50% chance of a yellow flickering light and a yellow still light, both of which provided reinforcement on 50% of presentations.

### Condition 2:

In this condition, the overall probability of reinforcement on the left lever was 20%. On the left lever, there was a 20% chance of a blue flickering light, and an 80% chance of a blue still light. The blue flickering light (S+) always provided reinforcement (100%), and therefore acted as a discriminative stimulus, and the blue still light (S-) never provided reinforcement (0%). The right lever stimulus light presentation and reinforcer percentages remained the same as in Condition 1.

### Condition 3:

In this condition, the stimulus and reinforcement probabilities were reversed from Condition 2. On the left lever, there was a 50% chance of a blue flickering light which provided reinforcement on 50% of presentations and a 50% chance of a blue still light which provided reinforcement on 50% of presentations. On the right lever, there was a 20% chance of a yellow flickering light (S+) which provided reinforcement on all presentations (100%), and an 80% chance of a yellow still light (S-) which did not provide reinforcement (0%).

Six sessions of reliable responding was used as the criterion for progressing to the next phase of the condition. The data from the first six sessions with two or more choice trials at each terminal link duration were analysed.

## Results

This experiment aimed to investigate the effect of decreasing terminal link duration on choice responding in a concurrent chains procedure. Terminal link duration, and stimulus and reinforcer probabilities were manipulated. Three primary dependent variables were measured: percentage choice towards the sub-optimal alternative; number of responses/response rate during the terminal link; and latency during the choice phase of forced choice trials (time from initial link response to terminal link response).

Choice data obtained during each session was converted into percentage choice towards the sub-optimal alternative. MATLAB software was used to gather relevant data from event data files to measure the number of responses towards each stimulus during the terminal link, and also to obtain latency data towards the optimal and sub-optimal alternatives in each choice phase. Responses during the terminal link and latencies to both alternatives for each trial were averaged to give one value per stimulus and per alternative for each session.

### *Training:*

Condition 1 served to identify whether any of the subjects would show a side bias, and to introduce the subjects to the delays to reinforcement occurring as a result of manipulating the terminal link duration. Training sessions were used to observe side biases, and experimental sessions were used to analyse percentage choice, latency, and response rate data. Figure 4 shows the percentage of left alternative choices during training. A9 showed a strong right bias during and following the 2-s training phase. A8 also showed a strong right bias from the 6-s training phase. A12 developed a right bias from the 6-s and 8-s training phases, and the 10-s experimental phase, which became much weaker when the terminal

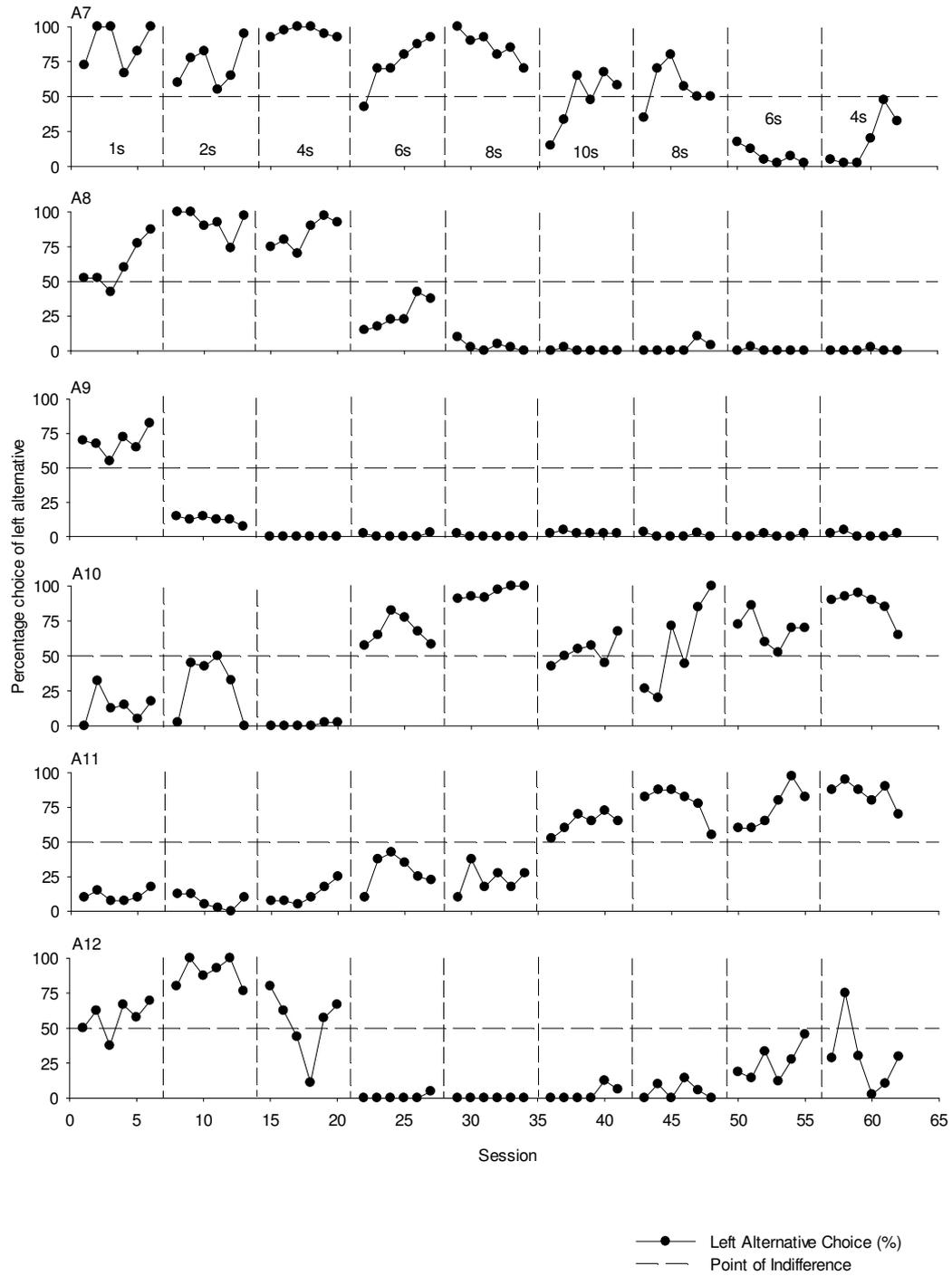


Figure 4. Percentage choice of the left alternative during Condition 1 experimental sessions and preceding training phases.

link duration was decreased. A10 and A11 eventually showed moderate left biases which took longer to form. A7 initially showed a left bias during 1-s to 8-s training phases. He became relatively indifferent during the 10-s and 8-s experimental phases, and developed a right bias in the 6-s experimental phase which decreased in strength in the 4-s experimental phase.

*Percentage choice of the sub-optimal alternative:*

Percentage choice has been analysed both including and excluding sub-optimal sessions. It was important to also report average data with sub-optimal sessions excluded as this type of choice responding was either observed in only one possums, or appeared to be a carryover effect from a previous condition, and therefore was not representative of all subjects.

Figure 5 shows the percentage choice of the sub-optimal alternative in Condition 2. All possums responded optimally across sessions with the exception of A7 responding sub-optimally from the third 6-s session onwards. Decreasing terminal link duration had no apparent effect. A7's preference for the sub-optimal alternative towards the end of Condition 2 affected the average. Figure 6 shows the average percentage choice of the sub-optimal alternative for all possums with A7s last 10 sessions in Condition 2 removed. On average, both with and without sub-optimal sessions removed, subjects showed a strong preference for the optimal alternative

Both A8 and A9 had strong right biases in Condition 1. This bias continued into Condition 2 and the beginning of Condition 3, more so for A8. Figure 7 shows the percentage choice of the sub-optimal alternative in Condition 3. On average, all possums responded optimally across sessions in Condition 3. A8 responded sub-optimally in the 10-s phase, and then began to respond

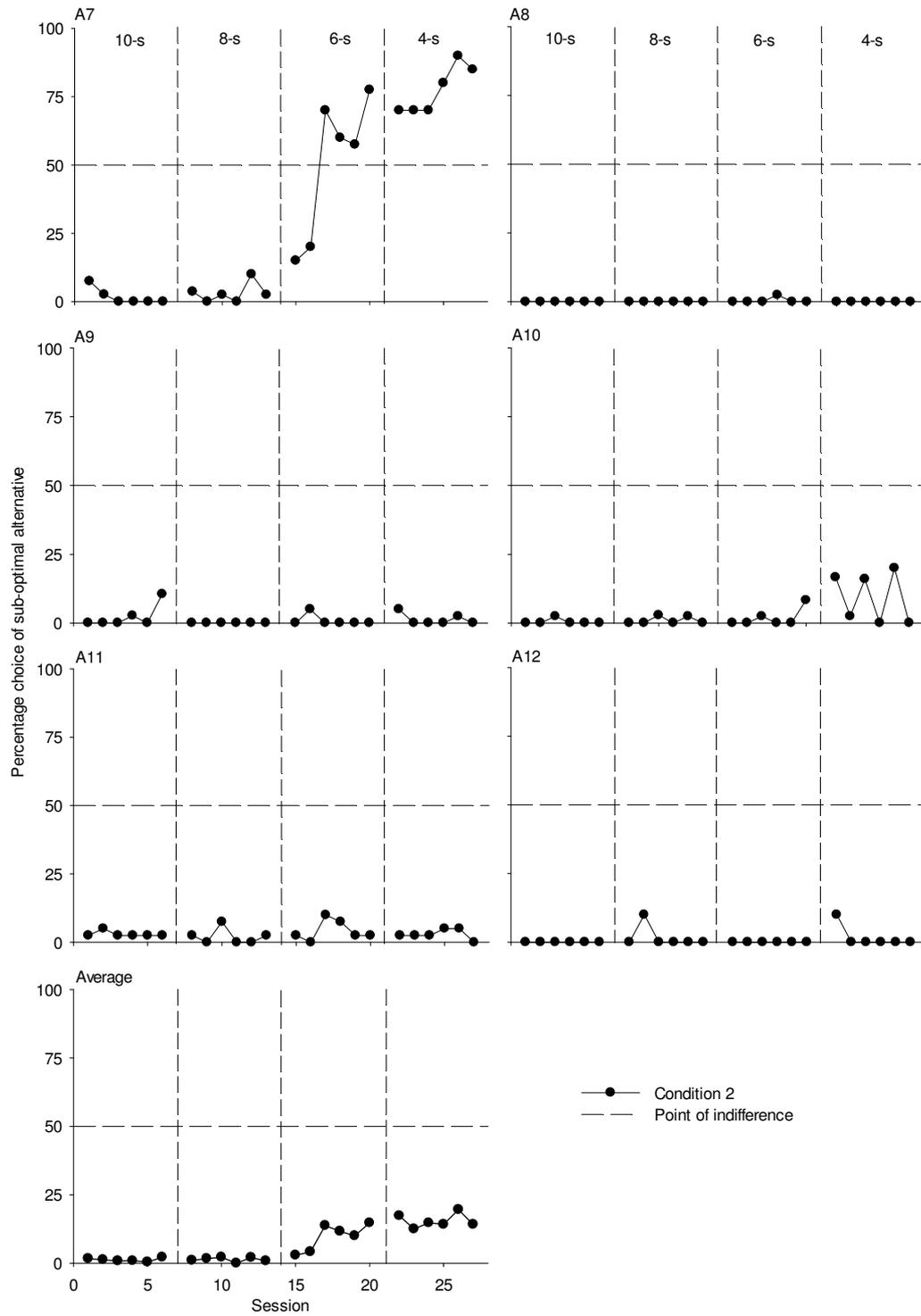
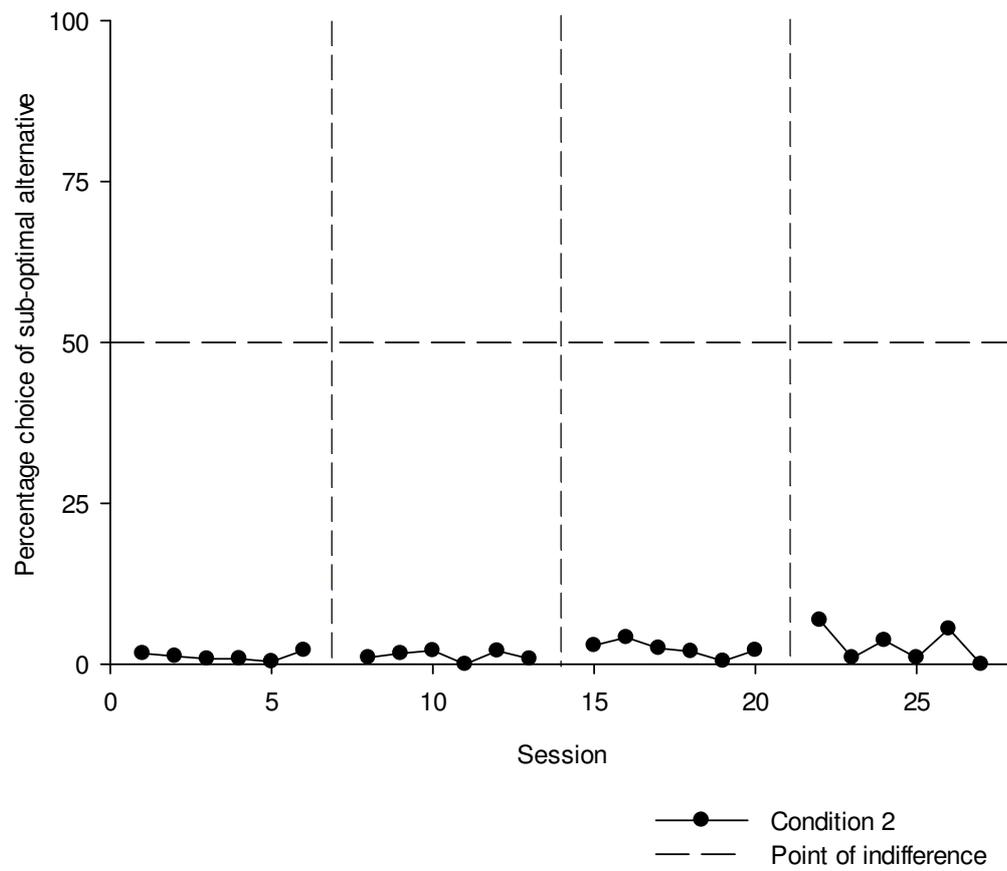


Figure 5. Percentage choice of the sub-optimal alternative in Condition 2.



*Figure 6.* Average percentage choice of the sub-optimal alternative across subjects in Condition 2 with A7 sub-optimal sessions removed

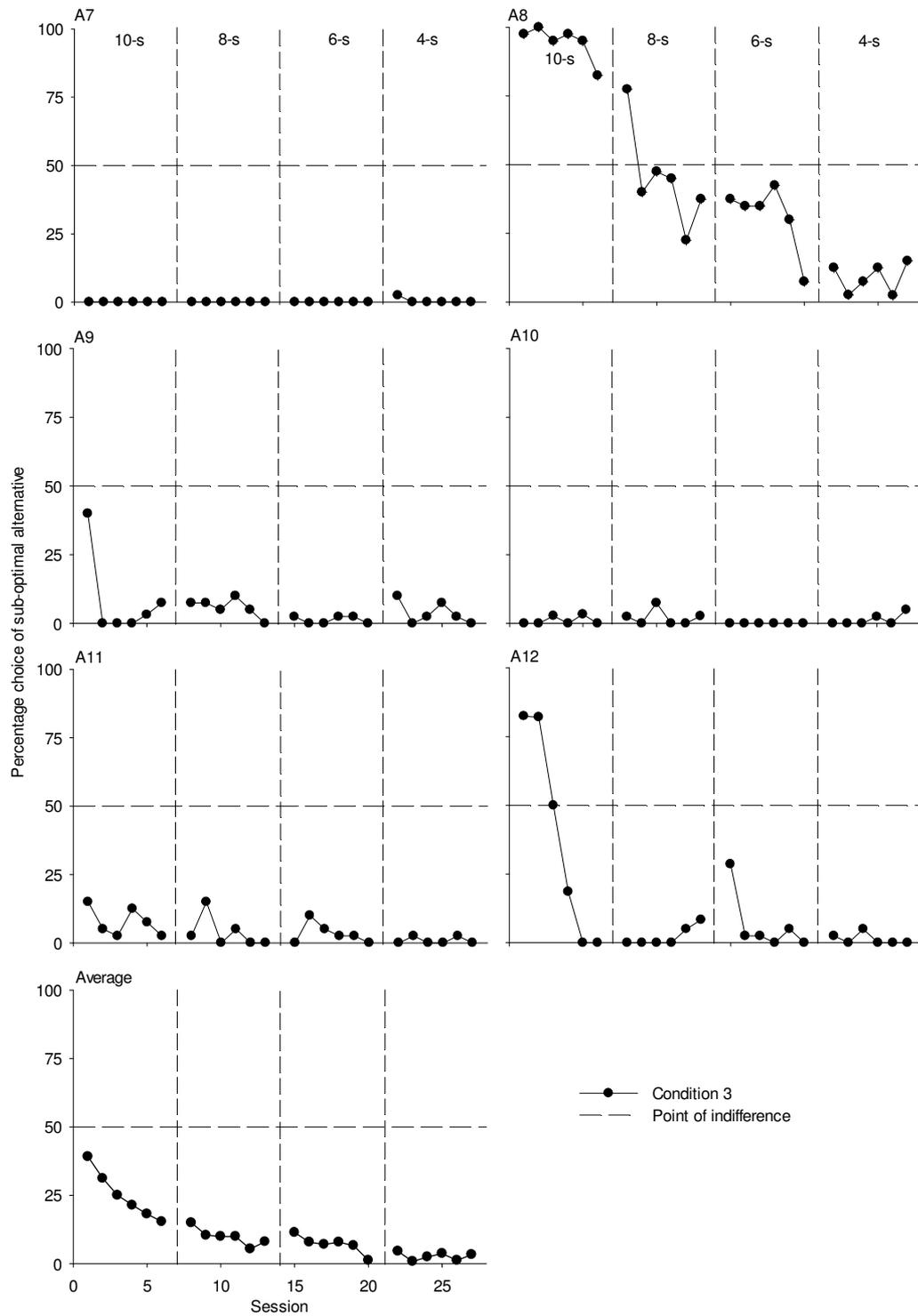


Figure 7. Percentage choice of the sub-optimal alternative in Condition 3.

optimally again, however, this preference was mostly moderate until the 4-s phase, where preference was still weaker than in Condition 2.

A comparison of percentage choice between Condition 2 and Condition 3 is provided in Figure 8. On average, subjects chose the optimal alternative more during 10-s and 8-s phases in Condition 2 than in Condition 3. They also chose the optimal alternative more during 6-s and 4-s phases in Condition 3 than in Condition 2. This average has been affected by A7 and A8s data.

Figure 9 shows the same data as Figure 8 with sub-optimal sessions from A7, A8, A9 and A12 removed. This was to account for the effect of A7 and A8's sub-optimal sessions on the averages. This resulted in the average choice percentage for Condition 2 and Condition 3 being very similar, with preference for the optimal alternative slightly higher in the 10-s, 8-s and 6-s phases in Condition 2 compared to Condition 3, and a slightly higher optimal preference in four of six sessions in Condition 3 compared to Condition 2 during the 4-s phase. Both with and without sub-optimal sessions removed, on average, the subjects showed a moderate to strong preference for the optimal alternative.

Comparison between 10-s and 4-s phases for Condition 2 and Condition 3 were examined to assess whether preference differed between these two terminal link durations. Figure 10 presents this comparison. In Condition 2, subjects showed a preference for the optimal alternative throughout the condition, and this preference was stronger during the 10-s phase than the 4-s phase. On average, the subjects also showed a preference for the optimal alternative in Condition 3, however, this preference was stronger during the 4-s phase than the 10-s phase. The averages were effected by A7, A8 and A12's sub-optimal data. These sessions were removed, and the data presented in Figure 11. With outliers

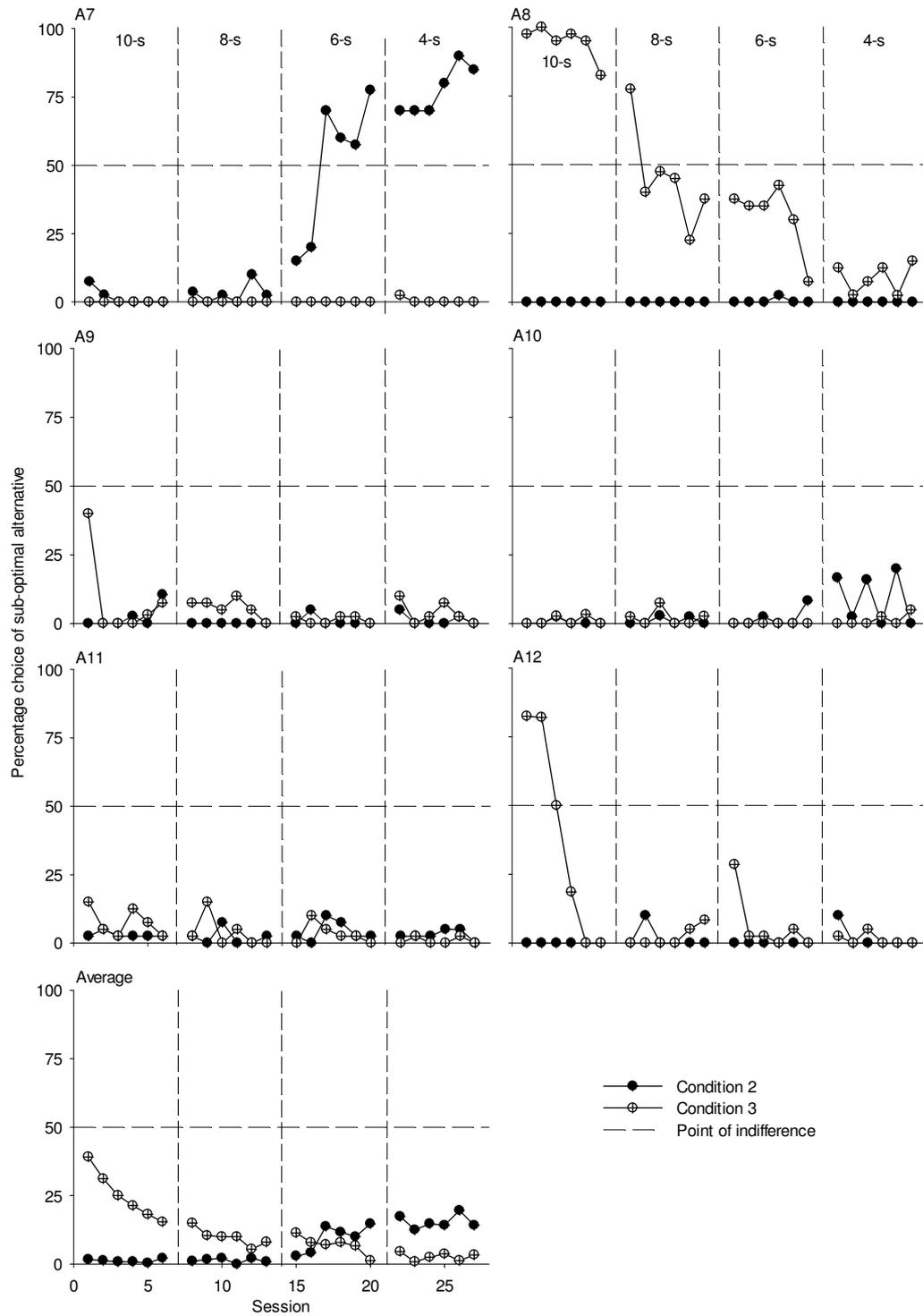


Figure 8. Percentage choice of the sub-optimal alternative in Condition 2 and Condition 3.

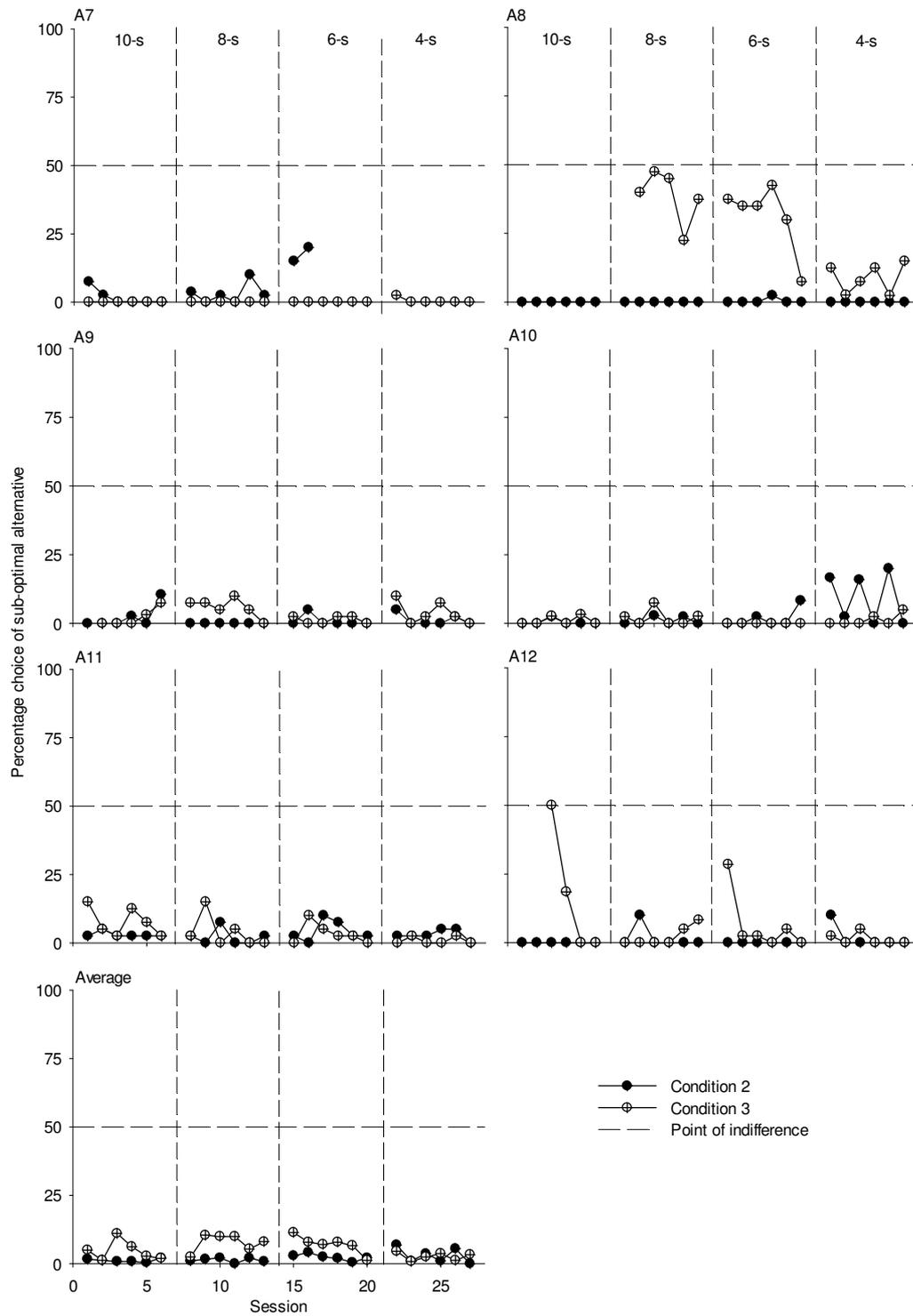


Figure 9. Percentage choice of the sub-optimal alternative in Conditions 2 and 3 with sub-optimal sessions removed

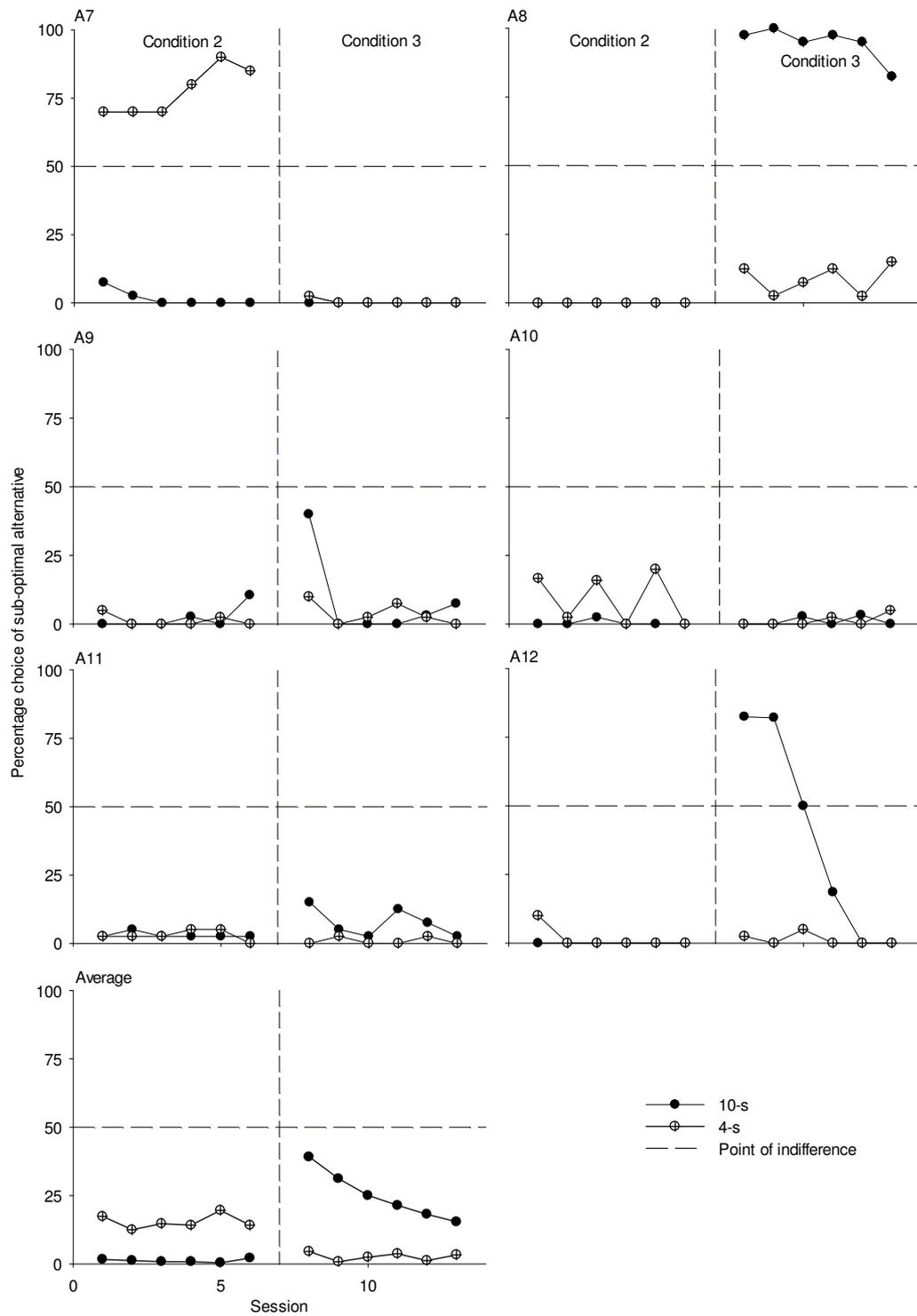


Figure 10. Percentage choice of the sub-optimal alternative at 10-s and 4-s in Condition 2 and Condition 3.

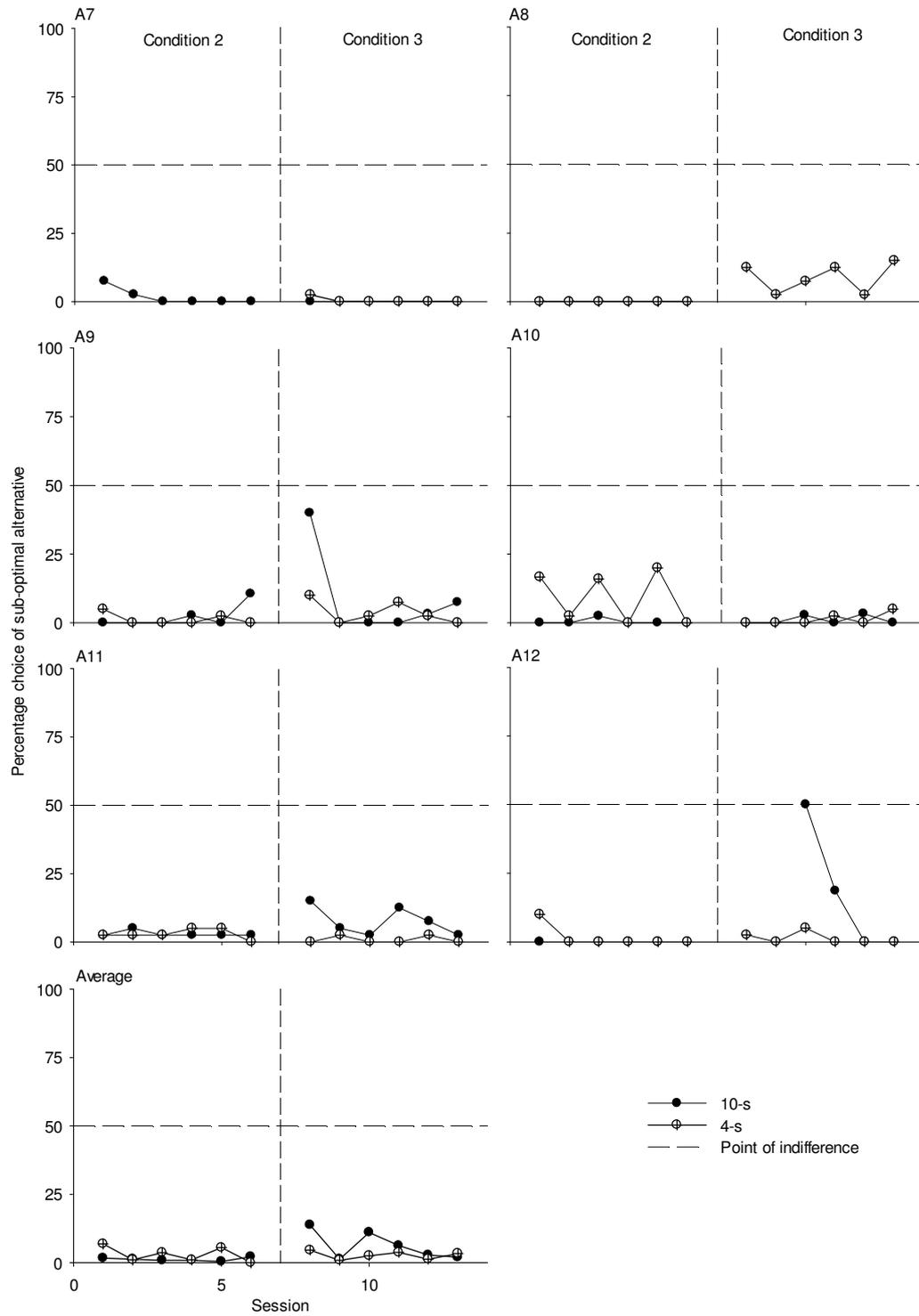


Figure 11. Percentage choice of the sub-optimal alternative at 10-s and 4-s in Condition 2 and Condition 3 with sub-optimal sessions removed.

removed, preferences were still the same on average, however these preferences were similar in both 10-s and 4-s phases of both Condition 2 and Condition 3

*Response rate:*

Figure 12 and Figure 13 show the average number of responses made per session towards the S+ and the S- during the terminal link in Conditions 2 and 3 respectively. As expected, the number of responses decreased as the terminal link duration was decreased, as there was less time for the subjects to respond. A7, A10, and A11 made more responses to the S-. However, on average, subjects responded more to the S+ during terminal links when compared to the S-. To better compare this difference both between and within conditions and phases, the number of total responses to S+ and S- stimuli were converted into response rate per session.

The S+ and S- response rates for Condition 2 and Condition 3 are shown in Figure 14 and Figure 15 respectively. On average, response rate was similar towards both the S+ and S- stimuli in Condition 2 as well as Condition 3. In Condition 3, A7 was the only subject with a clear difference in response rates towards the S+ and S- stimuli. His response rate was higher towards the S+ alternative for most sessions.

The response rate towards S+ and S- stimuli for Condition 2 and Condition 3 were converted into response rate difference between S+ and S-. Figure 16 and Figure 17 show the difference in response rate between S+ and S- stimuli in Condition 2 and Condition 3 respectively. A positive figure indicates a higher response rate towards the S+, and a negative figure indicates a higher response rate towards the S-. A7, A10 and A12 had higher response rates towards the S- in Condition 2. A8, A9 and A12 had higher response rates towards the S+ in

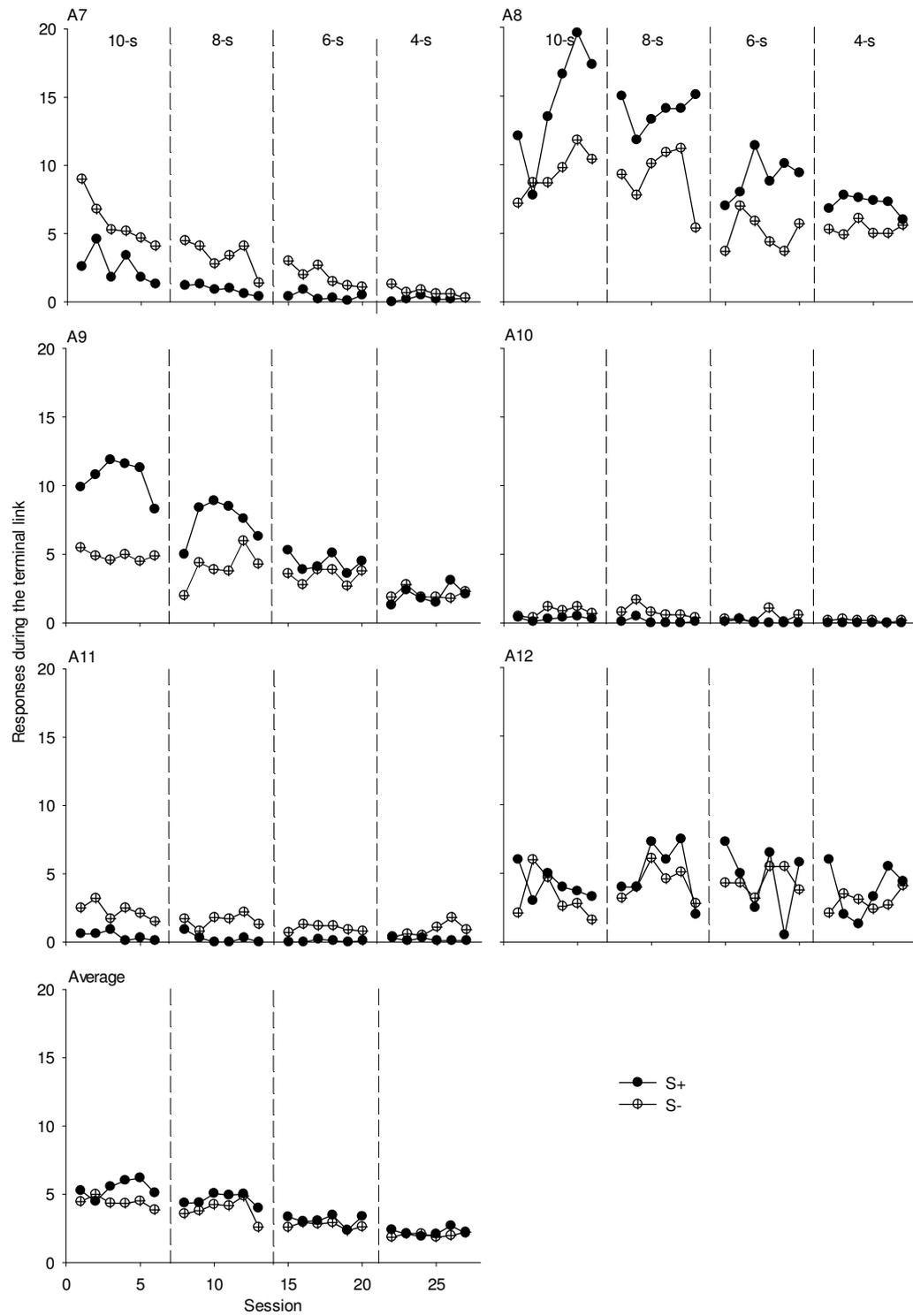


Figure 12. Responses to S+ and S- stimuli during the terminal link in Condition 2.

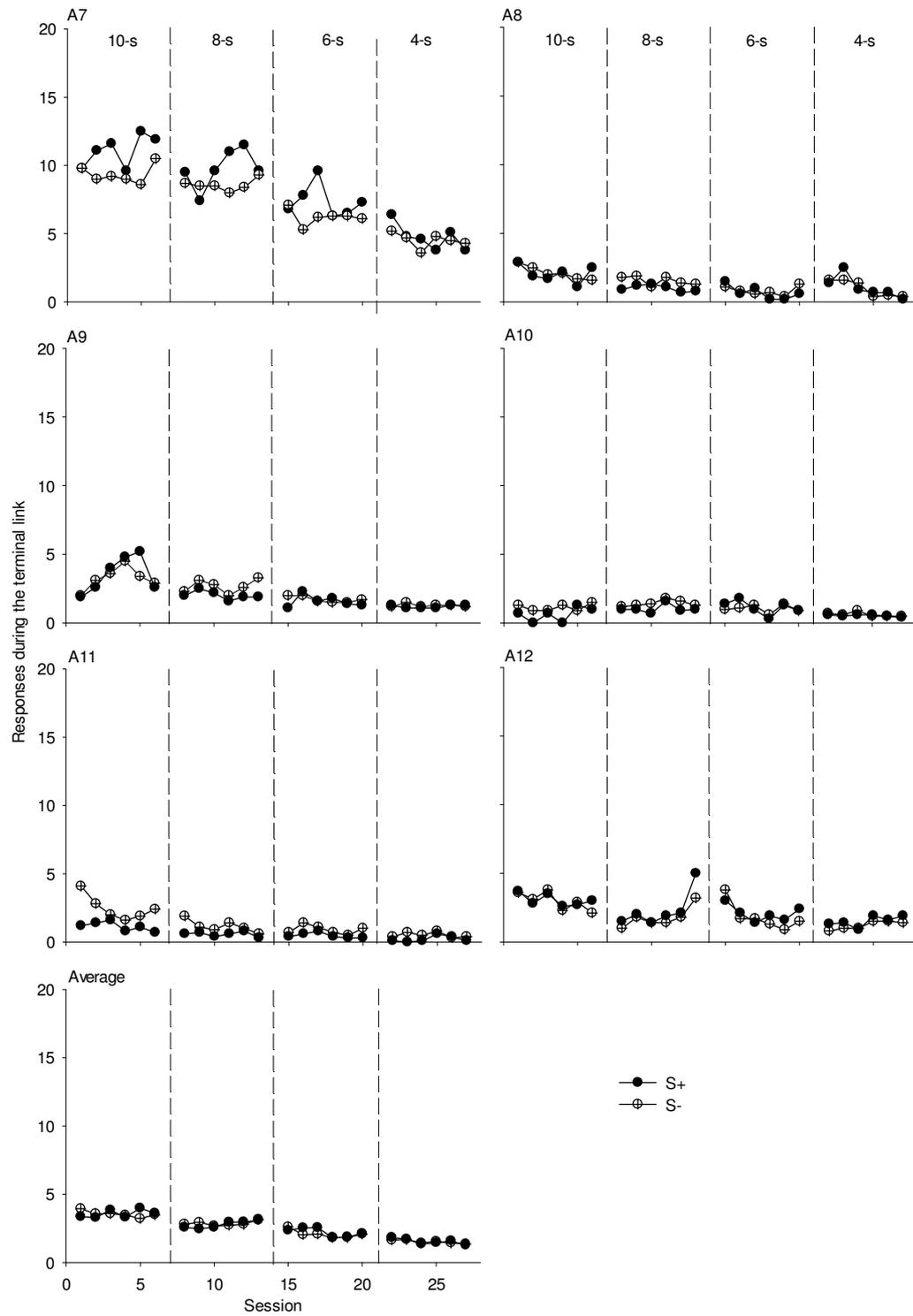


Figure 13. Responses to S+ and S- stimuli during the terminal link in Condition 3.

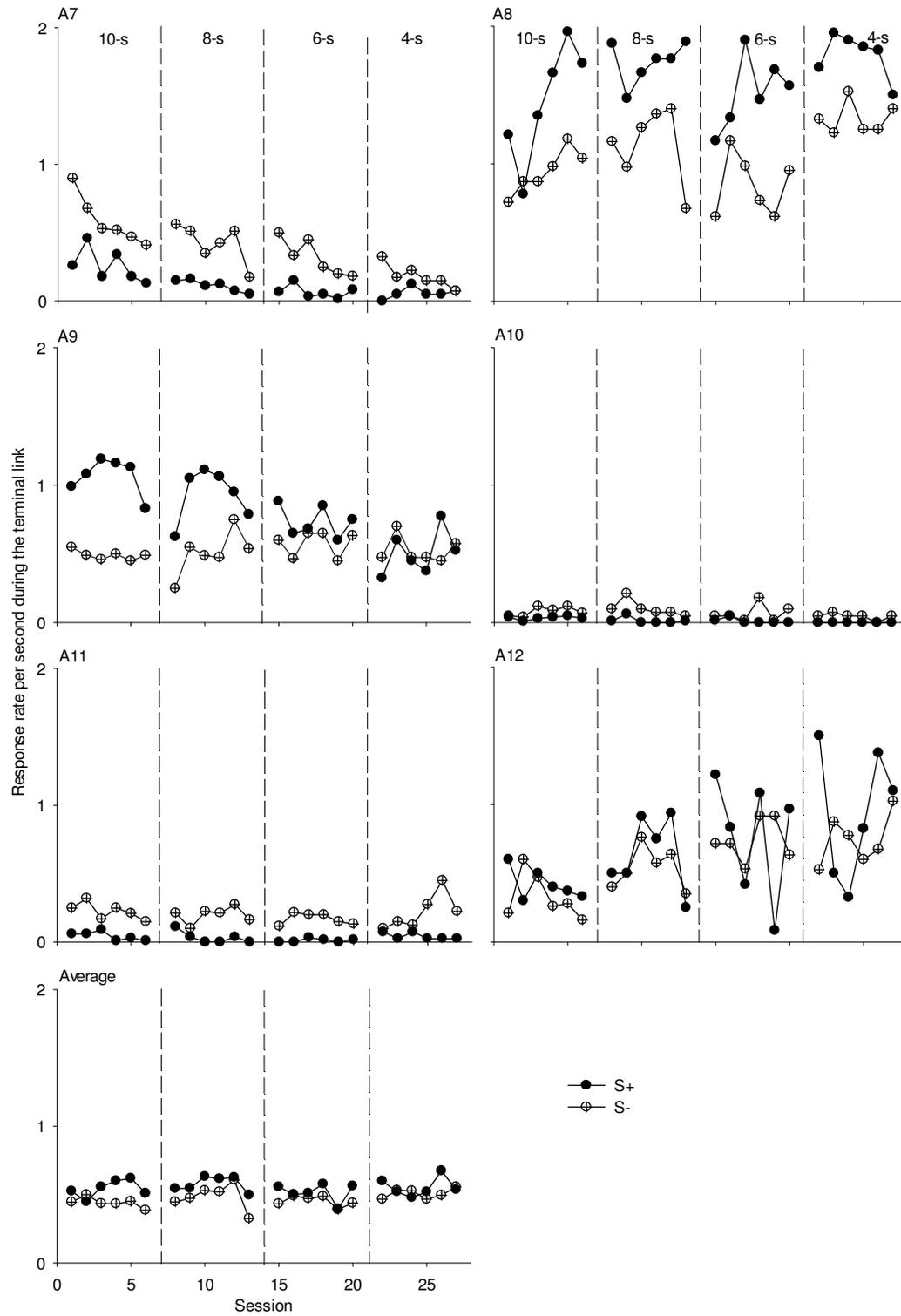


Figure 14. S+ and S- response rate in Condition 2

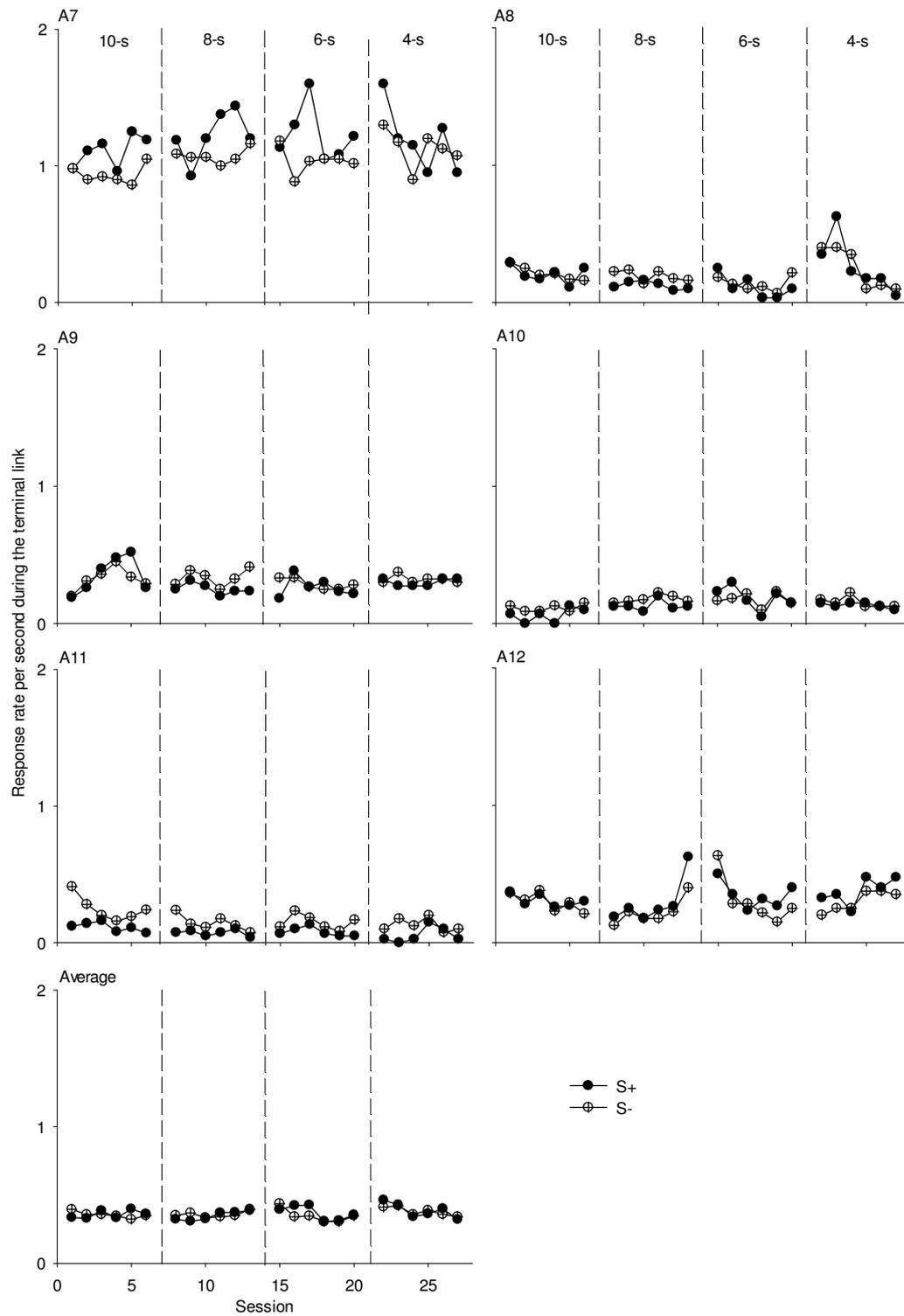


Figure 15. S+ and S- response rate in Condition 3

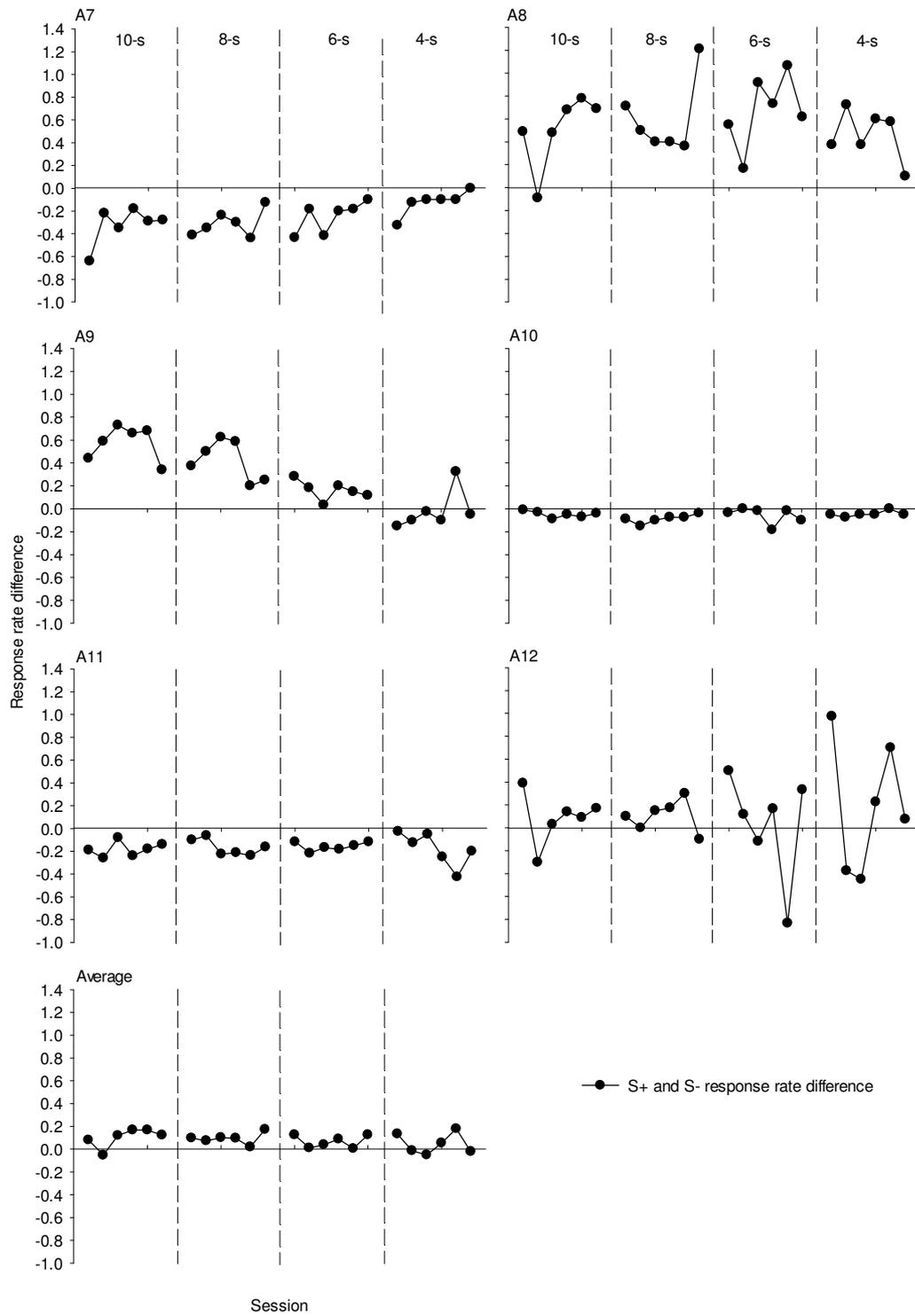


Figure 16. Difference in S+ and S- response rate in Condition 2

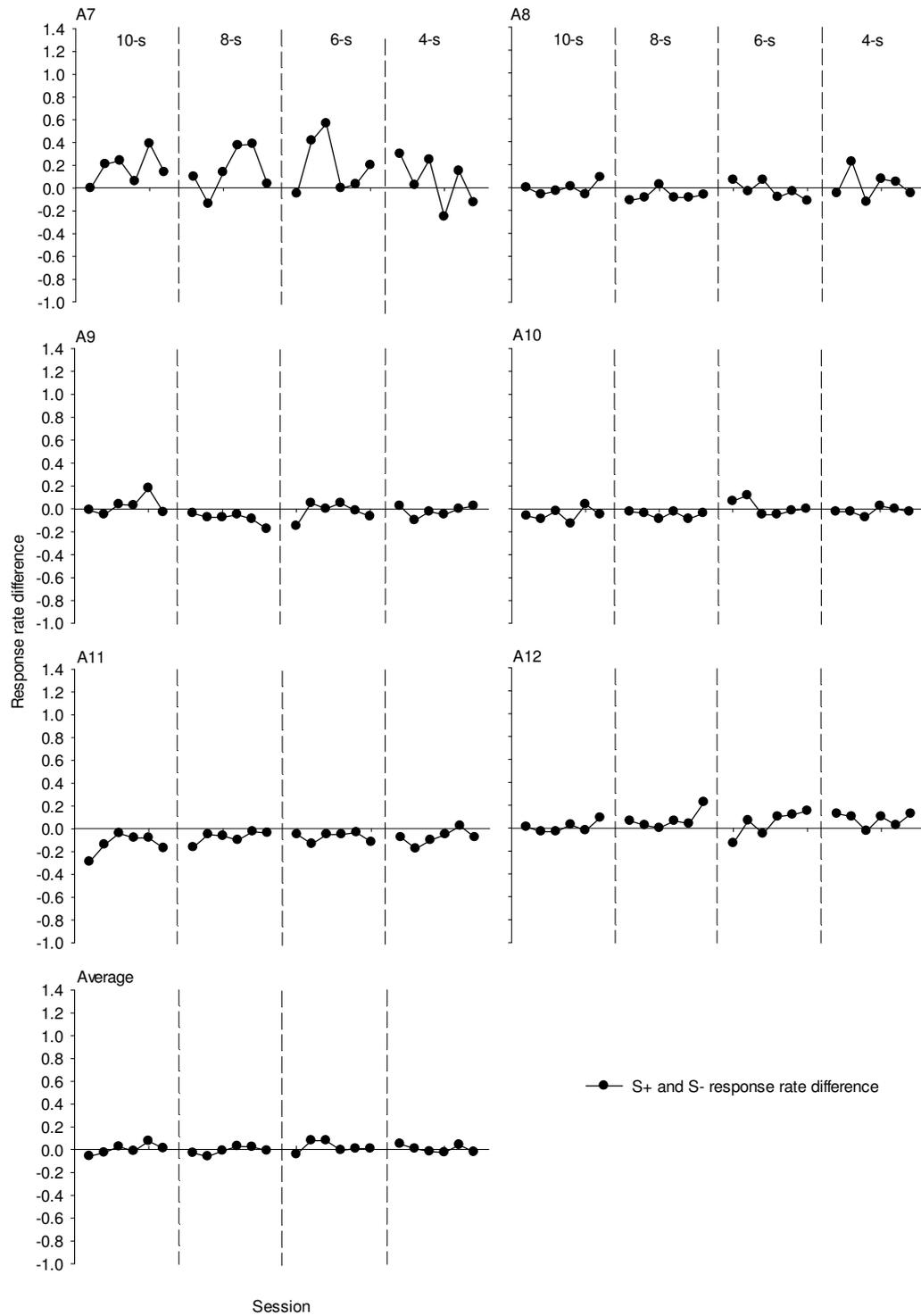


Figure 17. Difference in S+ and S- response rate in Condition 3

Condition 2. A8, A9 and A12's S+ response rates were higher than that of A7, A10 and A11's S- response rates, therefore on average, in all but 4 sessions response rates were higher towards the S+ in Condition 2.

In Condition 3, A7 and A12 had higher response rates towards the S+, and A8, A9, A10 and A11 had higher response rates to the S- in. A7's response rates towards the S+ were much higher than other subjects' response rates towards the S-, therefore on average, subjects responded indifferently towards the S+ and S- stimuli in Condition 3. In 12 sessions, response rates were higher for the S+, and in the remaining 12 sessions, response rates were higher for the S-.

As this experiment is investigating the effect of terminal link length, the response rates for the S+ and S- stimuli at 10-s and 4-s terminal link durations is presented in Figure 18. The difference in response rates from the 10-s phase to the 4-s phase was calculated for both S+ and S- stimuli in Condition 2 and Condition 3. These are presented in Figure 19, which clarifies the data presented in Figure 18. On average, subjects had a higher response rate towards the S- in the 4-s phase compared to the 10-s phase in both Condition 2 and Condition 3. Subjects' response rate differences were very similar in Condition 3. A10 and A11 responded similarly in both Condition 2 and Condition 3, however, there was a large variation in response rates differences in Condition 2 for A7, A8, A9, and A12.

*Latency:*

Latencies of choice trials were not examined. The sub-optimal alternative was often never chosen in choice trials in a session, resulting in a latency of 0-s. This would give the appearance that latency in the choice trial was low, and therefore reporting this would distort the results. For this reason, only forced

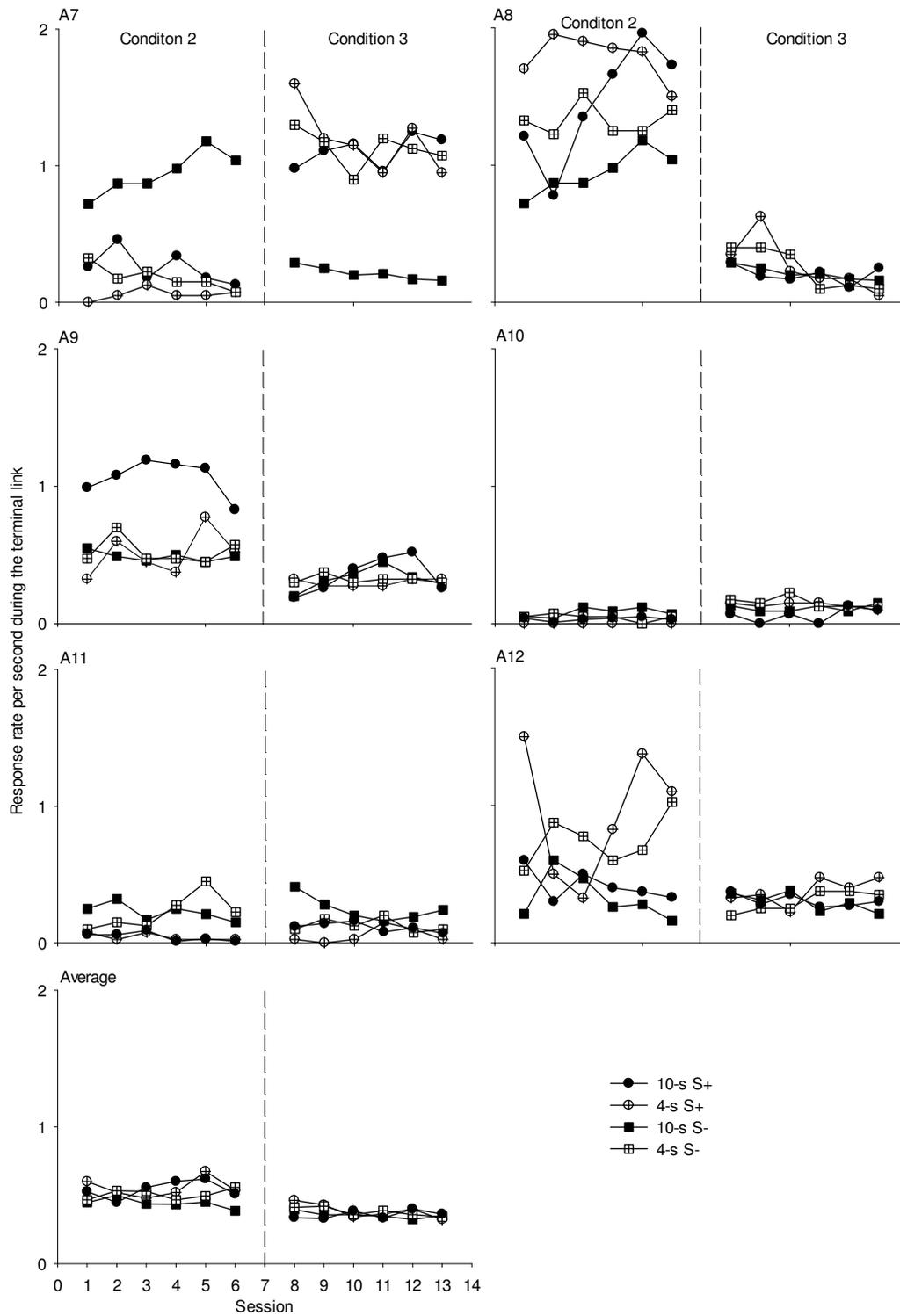


Figure 18. Response rate during the terminal link in 10-s and 4-s phases for both S+ and S- stimuli in Condition 2 and 3

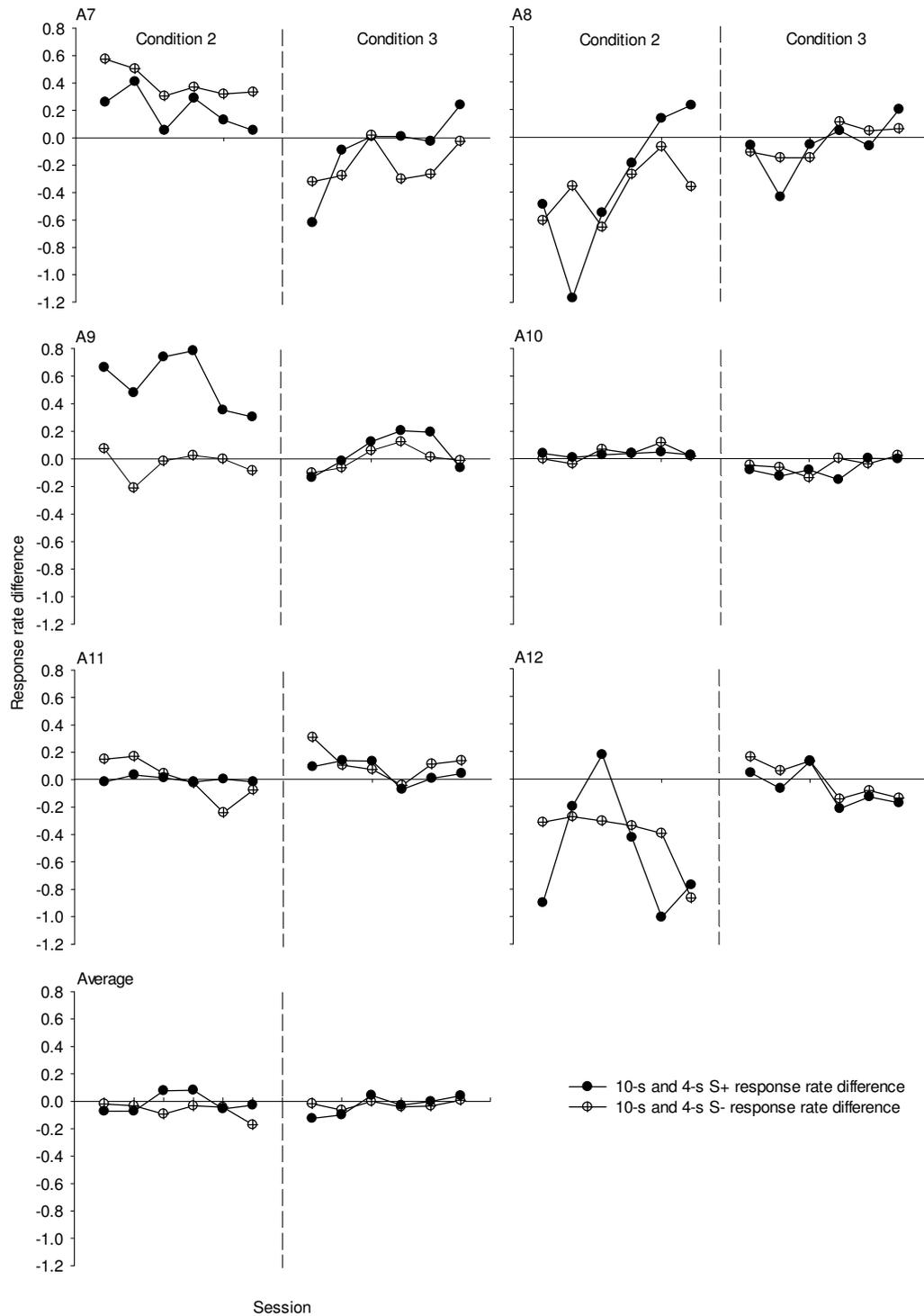


Figure 19. Difference in terminal link response rate between 10-s and 4-s phases for both S+ and S- stimuli in Condition 2 and 3

choice data was analysed.

Trials which had over 300ms latency between the initial link and terminal link (choice phase) were excluded from latency analysis as it is likely that the possums were not attending to the task for a period of time. Including these sessions would therefore distort the findings. On average, the number of trials per session removed during Condition 2 for A7 to A12 were 0.71, 2.63, 3.75, 2.42, 1.67, and 3.42 respectively. No trials were removed in Condition 3 for A9. An average of 2.42, 0.25, 2.58, 0.17, and 0.13 trials per session were removed for A7, A8, A10, A11 and A12 respectively.

Latency across session in the choice phase trials for Condition 2 and Condition 3 are presented in Figure 20 and Figure 21 respectively. In both Condition 2 and Condition 3, on average, latencies were higher in the choice phase when the sub-optimal alternative was available compared to when the optimal alternative was available. In Condition 2, the latency towards the sub-optimal alternative decreased as the terminal link duration decreased, however the latency towards the sub-optimal alternative in Condition 3 remained relatively similar across terminal link durations.

Figure 22 presents the latencies for the sub-optimal and optimal alternatives during 10-s and 4-s phases in Condition 2 and Condition 3. Both conditions show a similar trend in that the sub-optimal alternative has the highest latency in the 10-s phase, followed by the 4-s phase, however, 10-s sub-optimal latency is much higher in Condition 2. Latencies for the optimal alternative are lower than the sub-optimal alternative in both conditions. In Condition 2, the 4-s optimal latencies are higher than the 10-s optimal latencies, and in Condition 3, the 10-s optimal latencies are higher than the 4-s optimal latencies.

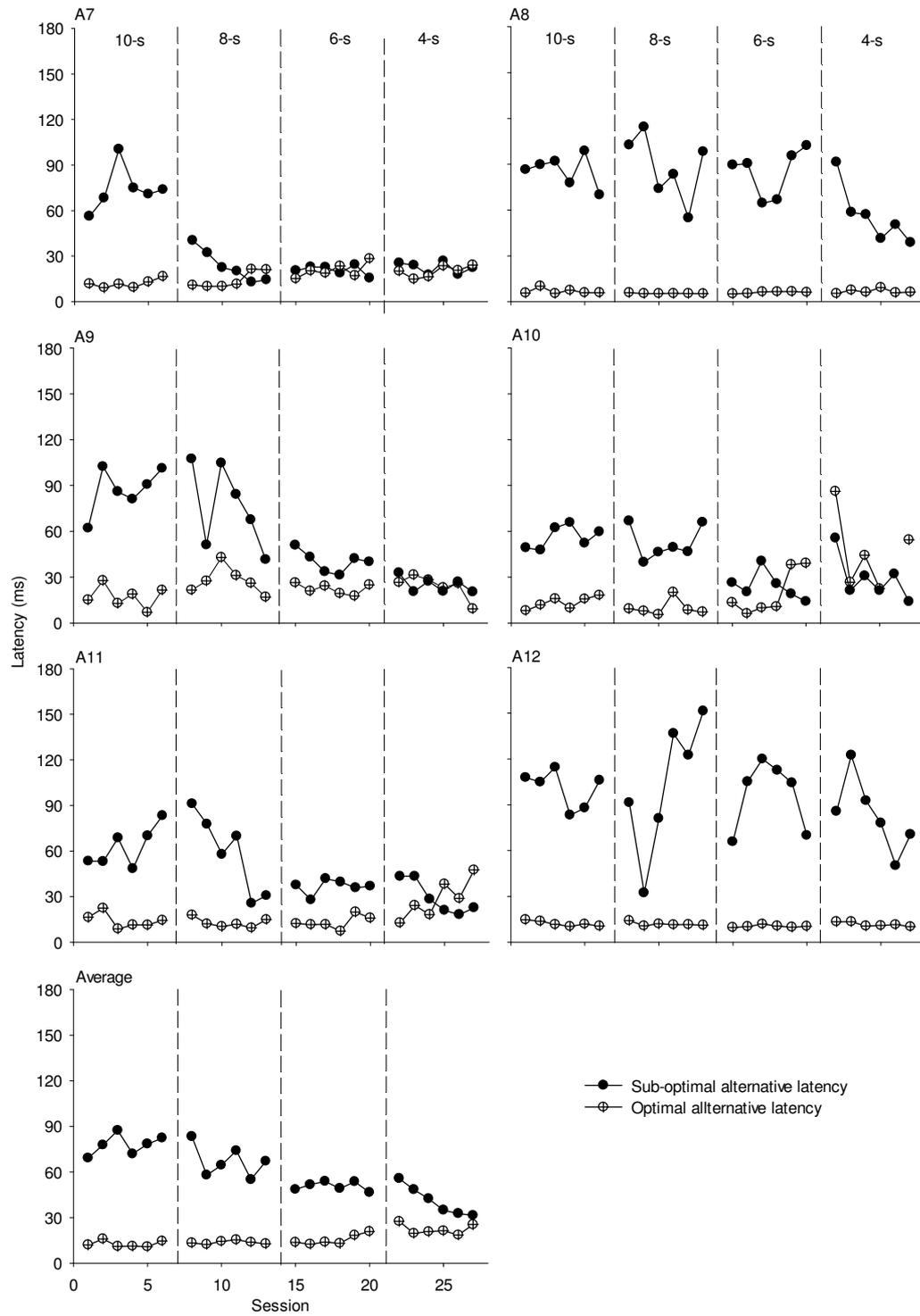


Figure 20. Choice phase latency for the sub-optimal and optimal alternatives in Condition 2.

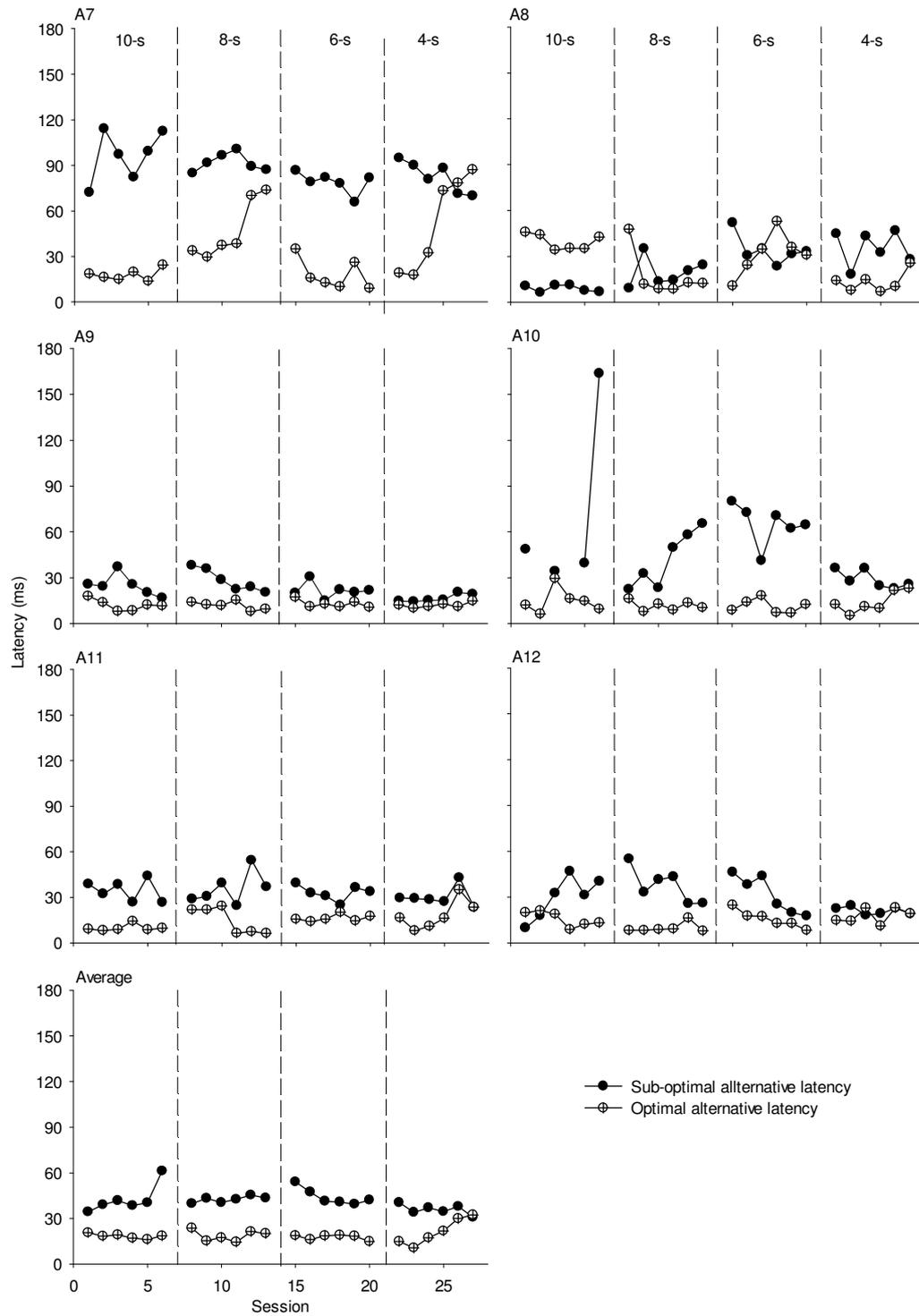


Figure 21. Choice phase latency for the sub-optimal and optimal alternatives in Condition 3.

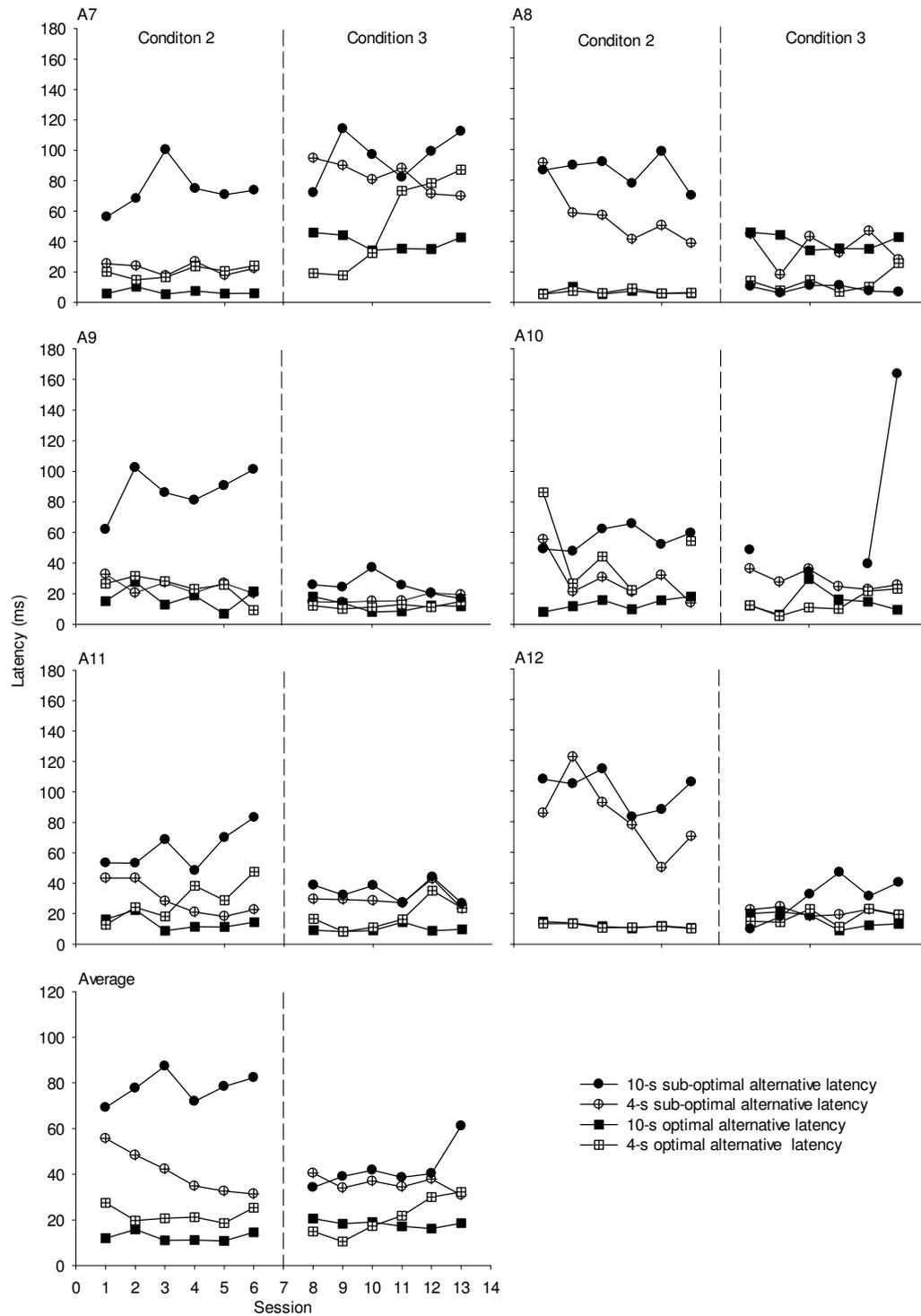


Figure 22. Choice phase latency for sub-optimal and optimal alternatives during 10-s and 4-s phases in Condition 2 and Condition 3.

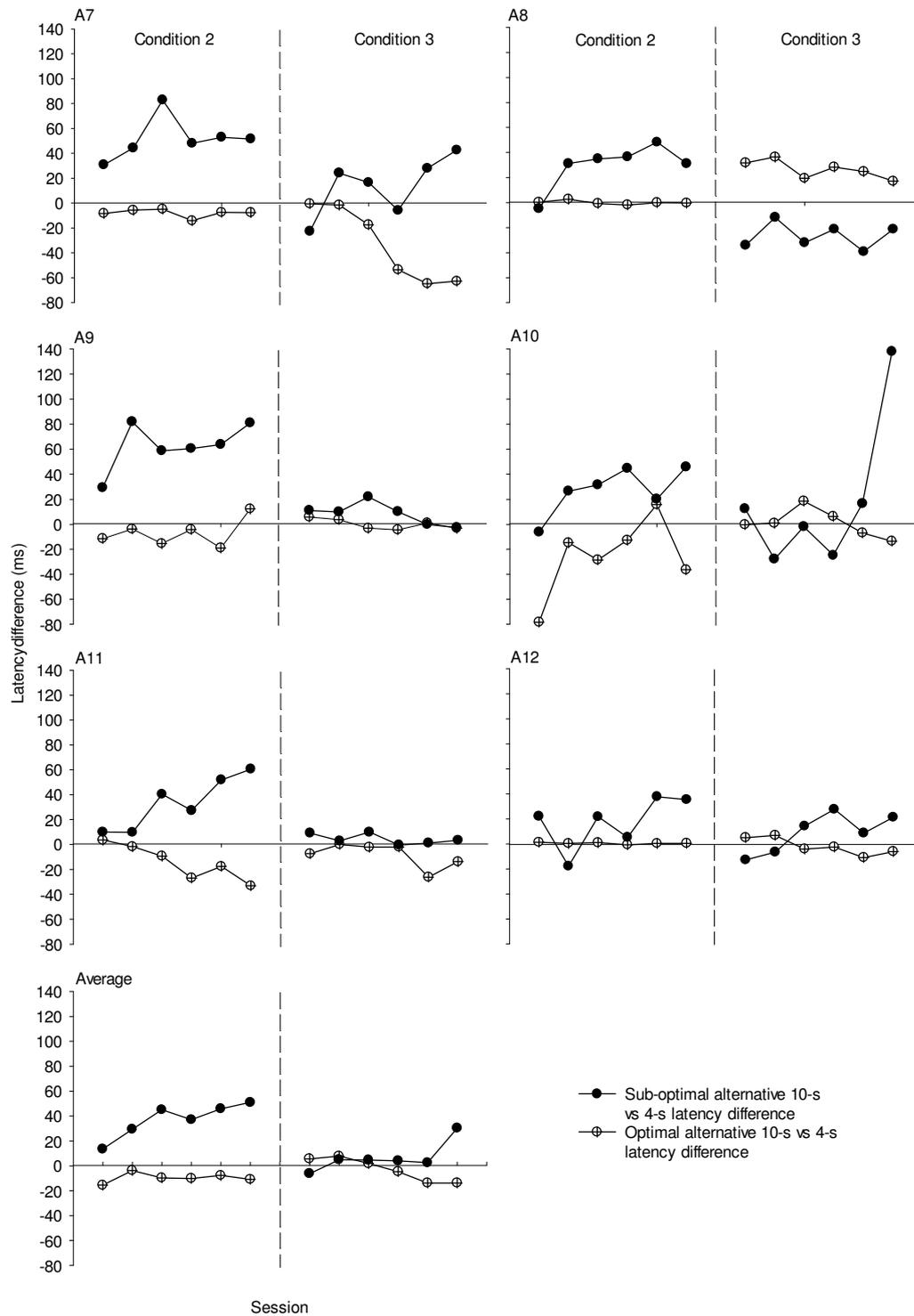


Figure 23. Difference in choice phase latency between 10-s and 4-s phases for both sub-optimal and optimal alternatives in Condition 2 and Condition 3.

The difference in choice phase latencies between 10-s and 4-s for both Condition 2 and Condition 3 are presented in Figure 23. A positive figure suggests that latency in the choice phase was longer in the 10-s phase than the 4-s phase, and a negative figure suggests that the latency in the choice phase was longer in the 4-s phase than the 10-s phase. On average, the sub-optimal latencies were higher than the optimal latencies, the sub-optimal 10-s phase had longer latencies than the sub-optimal 4-s phase, and the optimal 4-s phase had longer latencies than the optimal 10-s phase.

The difference between sub-optimal and optimal alternatives at 10-s and 4-s in Condition 2 and Condition 3 is shown in Figure 24. A positive figure suggests that latencies were higher for the sub-optimal alternative, and a negative figure suggests that latencies were higher for the optimal alternative. On average, latency was higher in both 10-s and 4-s phases for the sub-optimal alternative when compared to the 10-s and 4-s phases for the optimal alternative.

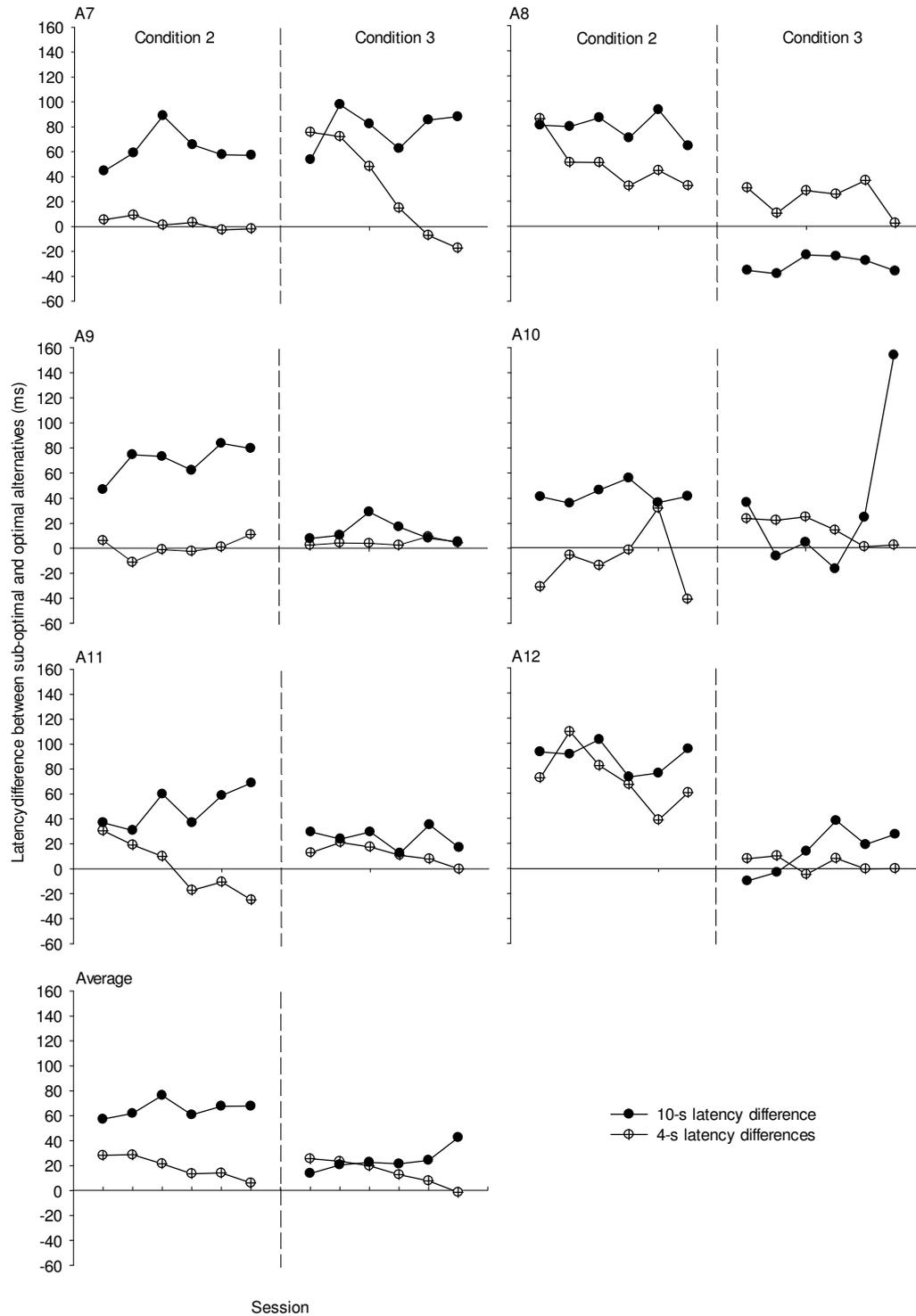


Figure 24. Difference in choice phase latency between sub-optimal and optimal alternatives during 10-s and 4-s phases in Condition 2 and Condition 3.

## Discussion

This experiment implemented a concurrent chains procedure which presented possums with a discriminative sub-optimal alternative and a non-discriminative optimal alternative, while simultaneously manipulating terminal link durations on both alternatives. This was to determine whether responding was controlled by discriminative stimuli, or overall reinforcement probability, and whether the same variable controlled responding at all terminal link durations. The probabilities of the stimuli and the probabilities of reinforcement were reversed, however the stimuli themselves remained on the same side. This was to examine whether the possums would continue to respond to the stimuli that had previously provided them more food, or whether they would follow the higher reinforcement rate.

Each possum was maintained at a weight at which they were motivated to work for the duration of the experiment. A small number of reinforcers (60 in Condition 1, and 48 in Condition 2 and 3) were available during the experimental sessions. The amount of reinforcement received during an experimental session was not enough to cause satiation. The 7200-s sessions allowed subjects enough opportunity to obtain the full amount of reinforcers at all terminal link durations without the experiment timing out. All subjects, except A12 regularly obtained the full amount of reinforcers, and rarely timed out. A12 was a small, elderly possum who regularly lost small amounts of weight. He therefore received more supplementary feed than necessary to maintain weight to encourage weight gain, and to maintain health.

It was hypothesised that possums would show a preference for the optimal alternative, and therefore response latencies to the optimal alternative would be

shorter than those towards the sub-optimal alternative. This preference was expected to be stronger at 10-s terminal link durations than at 4-s terminal link durations. It was also expected that if subjects were able to discriminate between stimuli on the sub-optimal alternative, response rate during the terminal link would be higher towards the S+ than the S-. The percentage choice towards the sub-optimal alternative, and the response latency data support the hypothesis, however response rates towards the S+ and S- were very similar. Theoretically, subjects should respond more to a stimulus that signals reinforcement compared to a stimulus that signals the absence of reinforcement. This suggests that subjects were able to discriminate between the alternatives based on overall reinforcement probabilities, but that they were unable to discriminate between the S+ and S- stimuli.

#### *Percentage choice*

In both Condition 2 and Condition 3, subjects responded optimally overall. In Condition 2, A8, A9, A11 and A12 showed consistently strong sub-optimal preferences. A10's preference for the optimal alternative weakened during the 4-s phase, however his preference for the optimal alternative was never below 80%. A7's preference reversed from optimal to sub-optimal during the 6-s phase and continued through to the end of the Condition. A7's responding is consistent with the results of Zentall and Stagner (2011a) who observed a preference reversal in pigeons when terminal link duration was incrementally decreased, however A7's initial preference was towards the optimal alternative, whereas the pigeons in Zentall and Stagner (2011a) initially responded sub-optimally.

The reason for the individual differences between subjects is unclear, as A7 did not show a preference in reversal in Condition 3. In Condition 3, all

subjects except A8 showed a strong preference for the optimal alternative with the exception of the first session for A9, and the first three sessions for A12. A8's responding is consistent with that observed by Zentall and Stagner (2011a) as he initially chose the sub-optimal alternative more than the optimal alternative, and began to choose the optimal alternative more as the condition progressed. A8's preference became optimal in the second session of the 8-s phase and remained optimal until the end of the Condition, however this preference was weak until the last session of the 6-s phase. This trend in responding was not observed in Condition 2, and can be explained by side bias. During Condition 1, A8 developed a strong right side bias. This bias was strengthened during Condition 2, as the right alternative was the optimal alternative, and therefore provided much more reinforcement than the already non-preferred side and alternative. This likely accounts for the slow preference reversal observed in Condition 3. A8's initial responding in Condition 3 should therefore not be considered preference for the sub-optimal alternative, as it appears to be a carry-over effect from Condition 1 and Condition 2. A8's slow preference recovery suggests that completing more training sessions when reversing alternatives to allow adequate experience with the schedule before collecting and analysing data, would eliminate carry-over effects from previous conditions.

The terminal link durations were manipulated to examine whether preference would differ between 10-s and 4-s phases in each condition. In Condition 2, preference for the optimal alternative was slightly stronger in the 10-s phase compared to the 4-s phase. This supports the hypothesis. However, in Condition 3, preference for the optimal alternative was slightly stronger in the 4-s phase than in the 10-s phase. The reason for this difference is clear.

Overall, the possums' choice responding, supports the hypothesis. It appears that subjects' responding was controlled by the overall reinforcement probability, rather than the discriminative stimuli. It is clear that subjects were able to discriminate between the alternatives, as when subjects were presented with a forced choice sub-optimal trials, they were observed responding aversively to the sub-optimal alternative, by moving to the nest box, or cage shelf, or performing behaviours which are typically aggressive, such as clicking, screeching, whistling and growling (Nowak, 1999). This aversion to the sub-optimal alternative is supported by the response latency data. It is not clear whether subjects were able to discriminate between the discriminative stimuli. Response rates towards during the terminal link were similar towards both the S+ and S-, suggesting that there was no perceived difference between the two stimuli.

#### *Responses/response rate*

As expected, the number of responses decreased as the terminal link duration was decreased, as there was less time for the subjects to respond. A7, A10, and A11 made more terminal link responses to the S- than the S+. However, on average, subjects responded more to the S+ stimulus during terminal links when compared to the S-. This is due to A8, A9 and A12 responding to the S+ at higher rates than A7, A10 and A11 responded to the S- in Condition 2. This difference was minimal, however. In Condition 3, on average, A7 and A12 had higher response rates towards the S+ stimulus, and A8, A9, A10 and A11 had higher response rates towards the S- stimulus. Averaged across subjects, response rates were equal towards both stimuli with a response rate difference of 0.01. Subjects therefore did not respond differentially between S+ and S- stimuli, making it unclear whether subjects were able to discriminate between the

individual stimuli and their reinforcement contingencies.

Singer and Zentall (2011) suggested that when delay to reinforcement was longer, the S+ was a stronger conditioned reinforcer than when they delay was shorter. This would suggest that more terminal link responses should be made to the S+ during the 10-s terminal link phase, and that the percentage choice of the sub-optimal alternative should be higher in the 10-s phase than all other phases. This was not reflected in my data. Response rates to the S+ stimulus during the terminal link fluctuated when terminal link duration was decreased in Condition 2, and terminal link response rate actually increased when the terminal link was incrementally decreased from 10-s to 4-s during Condition 3. This suggests that the delay to reinforcement did not affect terminal link response rate to S+ and S- stimuli.

#### *Latency*

Longer latencies were produced towards the sub-optimal alternative in all subjects. This suggests that conditioned inhibition occurred towards the less preferred alternative. Response rates during the terminal link did not show conditioned inhibition to S- stimulus when compared to the S+ stimulus. This further supports the idea that the possums were not discriminating between the stimuli on the sub-optimal alternative, but rather were discriminating between the overall reinforcement probabilities of both alternatives.

In Condition 2, latencies to the sub-optimal alternative decreased as the terminal link duration decreased, which is consistent with delay discounting – outcomes are delayed less steeply when they delay to reinforcement is shorter – however, no decreases in response latency were observed during Condition 3, as latencies remained similar across terminal link durations. It is unclear what caused

decreased latencies in Condition 2, and no change in latencies in Condition 3.

There are several variables which may partially account for the results observed, of which, impulsivity and level of deprivation appear to best explain the results of the current study, as well as the results of other studies with similar procedures, and different species.

#### *Deprivation levels*

In a natural setting, it is expected that animals will prefer a stimulus that is associated with 100% reinforcement (Laude et al., 2014). Laude et al. (2012) suggested that more hungry animals may attend to discriminative stimuli, whereas less hungry animals attend to overall rate of reinforcement - sub-optimal choice is more likely to occur at higher levels of food deprivation. It is therefore possible that the possums responded optimally as their supplementary feed was maintained at an amount at which they remained motivated to work, rather than at a pre-defined deprivation level, and their feed was almost always increased from week to week based on their weights. The possums' preference may have been different had they been more food deprived, and were therefore more likely to be influenced by conditioned reinforcers. The results of the current experiment are consistent with the idea of risk-sensitive foraging – animals are more likely to be risk-prone if they are in a negative energy budget, as taking a gamble and choosing the sub-optimal alternative is more adaptive for survival. Being in a positive energy budget does not require choosing the risky, larger payoff alternative, as survival is not at risk, hence why the possums showed an optimal preference. However, this does not account the fact that the pigeons in Laude et al's (2012) experiment received most of their food within the experimental session, and were therefore not in a negative energy budget.

Welte, Barnes, Wieczorek, Tidwell and Parker (2004) found higher rate of gambling in those of low socio-economic status. This could be accounted for by theories of deprivation, as energy budget is analogous to socioeconomic status. Those of low socio-economic status have less income, and are therefore money deprived. It is possible that when gambling, they attend to wins, and ignore losses, rather than attending to the overall ratio of wins to losses. Welte et al. (2004) suggest that those of high socio-economic status (analogous to a positive energy budget, and lower deprivation level) do not tend to develop pathological gambling behaviour, because they have the means to cope with losses obtained while gambling, whereas those of lower socio-economic status continue to gamble in an attempt to win back much needed income.

Examining choice responding at different deprivation levels would have given more insight into whether deprivation levels may account for choice responding in the current experiment.

The idea that animals who are at risk of starvation should choose the sub-optimal alternative (risky, but large) over the optimal alternative (would eventually lead to starvation) cannot be applied to studies which investigate 100% vs 50% reinforcement. This should theoretically only apply to studies which use different magnitudes when the unreliable outcome is actually larger than the certain outcome, which is not the case in Spetch et al's (1990) experiment.

The sociability of subjects has also been found to result in weaker sub-optimal preference, or optimal preference when compared to animals that are not socially enriched (Pattison et al., 2013). It is possible that because possums are not social animals, this effect would not be observed if they were placed under the same procedure (Laude et al. 2014). It is also not practical to place possums under

this same procedure in which they are able to interact with other possums as they are very territorial and are likely to injure each other.

The fact that social enrichment appears to inhibit, but not eliminate sub-optimal responding may provide insight for interventions for pathological gamblers (Pattison et al., 2013).

### *Risk sensitivity*

The possums optimal responding is further supported by hypersensitivity to risk due to their positive energy budget. Sub-optimal preference may result from hyposensitivity to risk and hypersensitivity to rewards (Zoratto, Sinclair, Manciooco, Vitale, Laviola, and Adriani, 2014). This can be applied to food deprivation levels. As previously mentioned, animals that are more deprived respond sub-optimally as responding to the risky alternative rather than the non-risky alternative may result in a positive energy budget, and therefore prevent starvation. Alternatively, animals that are less deprived, such as the possums in this experiment, respond optimally as they are risk averse, and do not need to respond to risky alternatives in order to maintain an energy surplus.

Bateson (2002) suggests that animal tend to avoid risk when the variance in choice comes from the amount of food provided by alternatives. This would suggest that animals will choose an optimal alternative, which provides a larger amount, or larger overall rate of reinforcement. This is consistent with the results of the current experiment.

Although risk sensitivity appears to provide a sufficient account for the results in the current experiment, Bateson (2002) suggests that the current explanations of risk sensitivity are not sufficient due to the various results found using different species and different procedures.

*Impulsivity, conditioned reinforcement, and lack of conditioned inhibition.*

Impulsivity has been found to affect responding in animals. Migo et al. (2006) found that the more impulsive an animal is, the less likely they are to produce conditioned inhibition towards an unprofitable stimulus or alternative. As the possums tended to be less impulsive due to their lack of food deprivation, their responding was self-controlled, and they were more likely to have developed conditioned inhibition towards the sub-optimal stimulus, which may account for their strong optimal preference.

Impulsivity provides a potential account for pathological gambling behaviour in humans, as pathological gambling behaviour has been found to result from lack of impulse control (Morasco, Weinstock, Ledgerwood & Petry, 2007). “Research on reward and punishment sensitivity in pathological gamblers has found that they have higher immediate reward sensitivity than controls” (Laude et al., 2012, p. 890). The lack of conditioned inhibition observed in this area may contribute to pathological gambling as only wins, which are conditioned reinforcers, are being attended to. Both pigeons who respond sub-optimally, and pathological gamblers do not appear to attend to losses (Pattison et al., 2013).

Zentall and Stagner (2011b) propose positive contrast as an explanation for the pigeons’ sub-optimal choice. In their experiment, the difference between the expected 20% probability of reinforcement, and a reinforced trial (100% probability, therefore 80% positive contrast) is much larger than the negative contrast following non-reinforcement (20% probability to 0% probability). This can be seen in human gambling through the expectation of wins versus actual wins as there is more positive contrast with win probabilities than negative contrast with expectation of losses and actual losses. Positive contrast did not

affect possums' responding. This suggests that positive contrast may not affect those with self-controlled behaviour, or those who are less deprived.

Conditioned reinforcement and conditioned inhibition occur in human gambling, for example, the visual effects of a slot machine. Stimuli which signal a loss occur more than those that indicate a win, and conditioned inhibition subsequently decreases with repeated exposure to these stimuli. This is further supported by the common finding that humans tend to focus more on wins than losses, and that pathological gamblers have reported getting enjoyment from the wins (Morasco et al., 2007). The results of Laude et al. (2014) support these hypotheses as they indicate that those who initially respond optimally in gambling situation may switch to sub-optimal responding due to decreased conditioned inhibition.

Consistent with the idea that stimuli are stronger conditioned reinforcers when they immediately signal trial outcome compared to when they are delayed, types of gambling that provide information about trial outcome instantly have been found to be more addictive than those that do not (Welte et al., 2004).

#### *Within and between species differences*

Much research with pigeons has found that they respond sub-optimally in various choice procedures Molet et al. (2012) found that when pigeons and humans were placed under the same magnitude procedure, pigeons had a much stronger preference than the participants in the self-reported "gambling" groups. Pigeons were reinforced with food, whereas humans were reinforced with points. The pigeons were therefore likely more motivated than the human participants, due to deprivation of motivating operation versus lack of motivating operations. These differences cannot be accounted for by varying deprivation levels as

theoretically, humans should have responded optimally because they were not deprived of reinforcement prior to experiment, however the gambling group responded sub-optimally when compared to non-gamblers. Gamblers' preference was technically indifferent when referring to percentage choice towards the sub-optimal alternative, however Molet et al. (2012) compared gamblers choice to non-gamblers choice, using non-gamblers as the baseline. It is possible that given more experience with the contingencies, the participants may have developed a stronger preference. They were only exposed to 20 forced choice and 20 choice trials in total, whereas pigeons in choice studies are typically exposed to thousands of trials.

Studies with pigeons have shown a decrease in conditioned inhibition produced by the S- with more experience of the reinforcement contingencies. Trujano and Orduna (2015) implemented a similar choice procedure with rats, and did not find this same decrease in conditioned inhibition which may account for why their rats responded optimally. It is likely that this can also account for the optimal preference shown by the possums in the current experiment.

ITI duration affects rats' preference, but not pigeons (Trujano et al., 2015). This is because altering the duration of the ITI alters the overall reinforcement rate of the session. Rats attend more to overall probability, whereas pigeons attend more to conditioned reinforcers. The possible effects of ITI were avoided in the current experiment as the ITI was held constant across phases and conditions.

The differences found between species suggest that the various choice procedures are not a good general model of human gambling. For this to be generalisable, a procedure needs to be developed in which all variables that appear to influence choice in several species can be examined.

Both Molet et al. (2012) and Zoratto et al. (2014) have shown that there can be within species differences in responding, and that the same species can often be divided into those who are risk prone, risk averse, and those who are neither.

#### *Differences in procedure*

Often choice procedures used with animals are said to be analogous of human gambling, although they do not replicate a real life gambling situation. Gambling typically involves choosing between two or more alternatives that do not guarantee reinforcement on a specific and consistent contingency (as is the case in sub-optimal choice procedures), and humans must forgo reinforcement (money in hand, or certain reward), to wager on each trial for a small chance to increase reinforcement.

Although much research around sub-optimal choice generalises its results to human gambling behaviour, little applied research with concurrent chains procedures has been conducted with humans.

Molet et al. (2012) note that differences in the procedures of their experiment, and those using pigeons, makes it difficult to compare their results with other studies, and generalise their findings between experiments and across species. This is an issue faced by numerous studies which have manipulated different variables. The results of these studies therefore may not generalise to real world gambling. Although some participants in Molet et al.'s (2012) experiment described themselves as gamblers, their gambling behaviour is likely not pathological, and it would be unethical to encourage gambling in those with an existing addiction.

Fantino and Abarca (1985) suggest that it is possible that the procedures

used in an operant setting with animals could result in behaviour that may not occur in natural settings, such as fixed reinforcement time and short experimental sessions, as opposed to 24 hour sessions to replicate foraging behaviour.

Vasconcelos et al. (2015) state that the issue with sub-optimal choice procedures is that they do not replicate natural foraging situations. In the wild, animals will cease work towards an opportunity that they know will not pay off, for example abandoning chase of prey that is going to escape. In the current experiment, possums were required to make the same number of response for both alternatives, and had to wait until the end of an un-reinforced trial before the next opportunity to gain reinforcement. They could not escape the current trial to reallocate work towards another alternative. Sub-optimal choice procedures also provide concurrent alternatives, whereas foraging in the wild is likely to involve opportunities that do not occur at the same time. However, adopting the operant procedures commonly used to investigate sub-optimal choice allows comparison with other works conducted in a similar manner. It is imperative to first establish internal validity within the conditions in which the experiment was conducted, before attempting to establish external validity in terms of generalising operant research to natural settings (Fantino & Abarca, 1985). However, it has been difficult to establish internal validity due to the contrasting results with different species, for example the differences observed between possums in the current experiment, and pigeons. Some operant research has introduced environmental variables to closer mimic foraging in natural settings. For example, Baum's (1982) experiment required increased movement within the operant chamber to simulate natural searching behaviour. This could potentially result in responding that differs from that observed in current procedures as it more closely resembles

a natural situation, however, the variables responsible for choice responding may not be certain until a procedure is developed in which internal validity can be established.

#### *Limitations and future research*

Time was a major constraint in this experiment. Given more time, several more manipulations could have been made to further investigate the effects of terminal link duration and percentage reinforcement on choice responding in possums.

A condition in which reinforcement probabilities were equal, but one alternative was signalled and one unsignalled would be interesting to implement. This would examine if discriminative stimuli are preferred when all other variables (terminal link duration, and reinforcement probability) remain equal, or whether, like the rats in Petri's (1974) study, possums would show a preference for the less informative alternative.

Two additional conditions in which the stimulus lights were reversed, as well as the probabilities of reinforcement could have been implemented to identify if the possums would follow the set of stimuli that have previously signalled optimal reinforcement, or if preference would remain with the larger overall rate of reinforcement. The current results suggest that it is likely that the possums would continue to prefer the higher probability as their preference followed the higher reinforcement percentage when the stimuli remained on the same side. It would also be interesting to examine whether preferences reversed at a different speed between reversing the stimulus light and reversing the reinforcement probabilities.

Manipulating terminal link duration of only the sub-optimal alternative

would have allowed closer comparison between Zentall and Stagner's (2011) results, and would have given more insight into which variables both controlled responding in possums, and influenced species differences.

To replicate real life gambling, animals could be placed in a procedure in which current wins could be wagered, for example one alternative could secure reinforcement for the previous trial, and another may have a double or nothing effect to observe the point at which animals will choose to keep the reinforcement they have gained. This would need to be conducted in an open economy as it would be unethical withhold supplementary feed from gambling animals who do not receive enough reinforcement to survive.

Real-life gambling situations can often present more than two alternatives. Introducing a third alternative in sub-optimal choice procedures may have an effect on choice responding. Bateson (2002) states that offering three (constant, less variable, and more variable), rather than two alternatives in a choice procedure has had interesting effects on preferred alternatives. They found that although all birds did not prefer the same alternative, introducing a third alternative strengthened each bird's preference for their initially preferred option (Bateson, 2002).

## Conclusion

Animal models of human gambling have highlighted several variables that are likely to influence choice responding in both animals and humans.

Impulsivity, and deprivation level appear to offer the best explanation of the findings in this area. The subjects in the current experiment responded optimally, which is consistent with theories regarding impulsivity and deprivation levels - less deprived animals are less impulsive, and do not rely on a risky reward for survival, and therefore will respond optimally. The possums' response latencies towards the less preferred alternative were longer than those towards the preferred alternative which is consistent with other research in this area. However, the terminal link response rates to S+ and S- stimuli were similar in both Condition 2 and Condition 3. Previous research has suggested that the S+ stimulus should be responded to more if subjects are discriminative between the two stimuli. A synonymous finding of the research reviewed is that the "underlying mechanism involved in suboptimal choice is unclear" (Laude et al., 2014, p. 10). The results of this study, along with previous research, shows that not all variables can be applied to research which implements different procedures and uses different species, however investigating varying levels of deprivation has provided the most probable explanation for the findings in this area.

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