Fax to: +496221/487-8686

Beate Gärtner
Springer-Verlag GmbH & Co. KG, Heidelberg

From:

Re: **Animal Cognition DOI 10.1007/s10071-003-0169-8**
Temporal landmarks: proximity prevails

Authors: **Fairhurst · Gallistel · Gibbon**

I. Permission to publish

Dear Beate Gärtner,

I have checked the proofs of my article and

- ❑ I have **no corrections.** The article is ready to be published without changes.
- ❑ I have **a few corrections.** I am enclosing the following pages:
- ❑ I have made **many corrections.** Enclosed is the **complete article.**

II. Offprint order

- ❑ Offprint order enclosed
- ❑ I do not wish to order offprints

Remarks:

Date / signature _____

III. Copyright Transfer Statement (sign only if not submitted previously)

The copyright to this article is transferred to Springer-Verlag (for U.S. government employees: to the extent transferable) effective if and when the article is accepted for publication. The copyright transfer covers the exclusive right to reproduce and distribute the article, including reprints, translations, photographic reproductions, microform, electronic form (offline, online) or any other reproductions of similar nature.

An author may make his/her article published by Springer-Verlag available on his/her home page provided the source of the published article is cited and Springer-Verlag is mentioned as copyright owner. Authors are requested to create a link to the published article in Springer's internet service. The link must be accompanied by the following text: "The original publication is available at http://link.springer.de or at http://link.springer-ny.com." Please use the appropriate URL and/or DOI for the article. Articles disseminated via SpringerLink are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks, and consortia.

The author warrants that this contribution is original and that he/she has full power to make this grant. The author signs for and accepts responsibility for releasing this material on behalf of any and all co-authors.

After submission of this agreement signed by the corresponding author, changes of authorship or in the order of the authors listed will not be accepted by Springer-Verlag.

Date / Author's signature _____

Journal: Animal Cognition
DOI: 10.1007/s10071-003-0169-8

Offprint Order Form

- To determine if your journal provides free offprints, please check the journal's instructions to authors.
- You are entitled to a PDF file **if you order offprints.**
- Please checkmark where to send the PDF file:

❑ galliste@ruccs.rutgers.edu

❑ _____

- If you do not return this order form, we assume that you do not wish to order offprints.
- If you order offprints **after** the issue has gone to press, costs are much higher. Therefore, we can supply offprints only in quantities of 300 or more after this time.
- For orders involving more than 500 copies, please ask the production editor for a quotation.

Please enter my order for:

	Copies	Price EUR	Price USD
❑	50	350.00	340.00
❑	100	400.00	390.00
❑	200	550.00	535.00
❑	300	700.00	680.00
❑	400	850.00	825.00
❑	500	1,000.00	975.00

Prices include surface mail postage and handling. Customers in EU countries who are not registered for VAT should add VAT at the rate applicable in their country.

VAT registration number (EU countries only):

_____

I wish to be charged in
❑ Euro
❑ US-Dollar

If not specified, invoices are made out in Euro.

Please indicate your institutional purchase order number (if any) here

_____

and send the purchase order, with all information about the article, via regular mail. The author will be billed for orders without a purchase order number. The title of the journal and the manuscript number of the article must be stated on the purchase order.

❑ Please charge my credit card
  ❑ Eurocard/Access/Mastercard
  ❑ American Express
  ❑ Visa/Barclaycard/BankAmericard

Number (incl. check digits):

_ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _ _

Valid until: _ _ / _ _

Signature: _____

Send invoice to:

❑ C.R. Gallistel
Rutgers University
Department of Psychology
152 Frelinghuysen Road
Piscataway, NJ
08854-0820, U.S.A.

❑ _____

Ship offprints to:

❑ C.R. Gallistel
Rutgers University
Department of Psychology
152 Frelinghuysen Road
Piscataway, NJ
08854-0820, U.S.A.

❑ _____

Date / signature: _____

Animal Cognition
© Springer-Verlag 2003
DOI 10.1007/s10071-003-0169-8

Original Article

Temporal landmarks: proximity prevails

S. Fairhurst · C. R. Gallistel (✉) · J. Gibbon

S. Fairhurst · J. Gibbon
New York State Psychiatric Institute, 1051 Riverside Dr., Unit 50, New York, NY 10032, USA

C. R. Gallistel
Department of Psychology and Rutgers Center for Cognitive Science, 152 Frelinghuysen Rd, Piscataway, NJ 08854-8020, USA

✉ C. R. Gallistel
Fax: +1-732-4458085
E-mail: galliste@ruccs.rutgers.edu

Received: 18 September 2003 / **Revised:** 25 March 2003 / **Accepted:** 31 March 2003

Abstract Subjects in conditioning experiments time their conditioned responses relative to the onsets of the conditioned stimuli (CSs). These onsets are temporal landmarks, by reference to which subjects may estimate the location of the unconditioned stimulus (US) in time. In a serial compound conditioning paradigm, a long duration CS comes on first, followed later by a second shorter CS, creating both a long-range and a short-range predictor of the US. We ask whether displacing the short-range predictor relative to the long-range predictor causes subjects to strike a compromise between the different temporal locations predicted by the two CSs. In three experiments with pigeons, we varied the training conditions so as to favor or militate against this outcome. However, in all conditions, there was no compromise; after the onset of the displaced short-range CS, the timing of conditioned responding was governed by it alone. This result contrasts with the compromises that are seen when the feeding time predicted by a CS is put in conflict with the time predicted by the circadian clock, and with the similar compromises sometimes seen when a nearby spatial landmark is displaced relative to a larger spatial context.

Keywords Timing · Temporal context · Serial compound conditioning · Occasion setting

John Gibbon died while this work was being prepared for publication

Introduction

The conditioned stimuli (CSs) in operant and Pavlovian conditioning are landmarks in time, by reference to which the subject may estimate where in time an unconditioned stimulus (US) will occur (Gallistel and Gibbon 2000). The location of the US in time may be estimated by its (temporal) distance from CS onset, just as the location of a US in space may be estimated by its (spatial) distance from a landmark (Honig 1981; Srinivasan et al. 1997; Collett et al. 2002). Spatial landmarks often function within a larger framework (a landscape). When they are displaced relative to that framework, the location at which a subject searches is sometimes a compromise between the location relative to the landscape (larger framework) and the location relative to the landmark (e.g., Cheng 1989). On the other hand, when bees must estimate the distance to fly down a tunnel to reach a food source, landmarks near the source dominate behavior. There is no compromise when the distance from a near landmark conflicts with the distance from a landmark farther back in the tunnel; the distance from the near landmark determines where they stop to search for the food (Srinivasan et al. 1997; Collett et al. 2002).

Gibbon et al. (1997) reported a compromise in the temporal domain, with circadian time serving as the larger framework. The temporal landmark that operated within this framework was the illumination of a key, which occurred at three fixed times of day. It signaled to pigeon subjects 30 min of food availability, beginning 30 min after CS onset. They obtained the food by pecking the key. On infrequent probe trials, the food was not forthcoming, and the CS remained on for 2 h. Subjects' tendency to peck the key on these probe trials peaked 30 min after CS onset (location relative to the CS), then declined. Because the CSs occurred at fixed times of day, these peaks also coincided with a particular phases of the subject's circadian cycle—locations within that cycle. When the CSs were displaced by an hour relative to the circadian cycle, the time at which pecking peaked was a compromise between the expected circadian location of food onset and its expected location relative to CS onset.

The circadian timing framework was shown to have two components, which specify location within that framework by two different timing mechanisms. One component was the entrained circadian cycle. Locations within this cycle are specified by a mechanism that records the phase of the cycle at the moment when food becomes available and compares the current phase of the cycle (the subjective time of day) to the remembered time of day (for review, see Gallistel 1990; for a different conception of the causation of circadian anticipatory activity, see Mistlberger 1994). The other component was the lights-on (objective dawn) in the light-cycle that entrained the circadian rhythm. The time of day may also be estimated by timing from this landmark. Occasional probe days, on which dawn was advanced or retarded by 60 min or longer, displaced this interval–timing framework relative to the endogenous circadian cycle. On these probe days, the timing of the first peak (the "breakfast" peak) was a compromise between the location predicted by the endogenous cycle and the location predicted by interval timing from dawn. By contrast, the timing of the two later peaks (lunch and dinner) was dominated by the location within the circadian cycle.

These results raise the question whether similar compromises are observed when only short-interval timing is involved. When the onset of a CS that predicts food after a short latency occurs within the context of a second CS with an earlier onset, does displacing the short CS within the framework established by the long CS lead to a compromise between the predicted temporal locations?

This question may also be posed within the context of what is known about the occasion-setting phenomenon, which occurs in serial compound conditioning. In an occasion-setting paradigm, the proximal CS, whose onset is relatively close in time to the US, predicts the US only on those trials on which the onset of the proximal CS has been preceded by the onset of an occasion-setting stimulus. Although, the occasion-setting stimulus does not, by itself, elicit a conditioned response, it exerts higher-order control over the conditioned response to the proximal CS. The subject responds to the proximal CS only when the occasion has been set by the earlier onset of the occasion-setting stimulus (Holland 1983).

The latency of conditioned responses are generally proportionate to the CS-US interval (Gallistel and Gibbon 2000; Savastano and Miller 1998), which is why it is appropriate to think of the onset of the CS as a landmark in time. The occasion-setting effect also shows temporal specificity: it is greatest when CS onset follows the onset of the occasion-setter at the usual (training) interval (Holland et al. 1997). Thus, the question arises whether, when the CS comes on at the wrong time relative to the onset of the occasion-setter, does the

timing of the conditioned response reflect a compromise. This is a different question from the question whether the capacity of the CS to elicit a conditioned response depends on where its onset occurs relative to the occasion-setter. In the one case, the focus is on the strength or probability of the conditioned response. The question we pose concerns its timing.

In these experiments, we varied conditions so as to make a compromise in the timing of the conditioned response increasingly likely. We find, however, that under all the conditions we tried, the location of the peak probability of response is entirely determined by the CS whose onset is closer in time to the predicted feeding, even though, under our conditions there is an (appropriately timed) conditioned response to the longer CS in the baseline conditions. Thus, when a more proximal temporal landmark occurs, it completely controls the timing of the conditioned response.

Methods

Subjects

Subjects were 8 White Carneau pigeons maintained at 80% of ad lib body weight. All subjects had previously served in an autoshaping experiment.

Subjects were individually housed in a separate colony room with free access to water at all times. Lights in the colony room switched on at 7:00 a.m. and off at 7:00 p.m. Sessions were run 5 days a week at approximately the same time of day.

Apparatus

The experimental chamber was a standard Lehigh Valley Electronics pigeon-conditioning chamber. The subject space was 30 cm long, 34 cm wide, and 34 cm high. An aluminum wall of the chamber had three response keys, each 2.5 cm in diameter and mounted 25 cm above a mesh floor. Each key could be transilluminated by an IEEE projector. Only the center key was operative in this experiment. An aperture (5 cm by 5 cm) centered 10 cm above the floor provided access to a solenoid-operated grain hopper. A 15-W houselight was mounted in the same wall, 32 cm above the floor. An externally mounted fan provided ventilation and masking noise. The chamber was housed in a light- and sound-attenuated room. The CSs were two different patterns of key illumination—a homogenous red field and an X.

Procedure

Subjects were divided into two groups of four birds each. The birds in group A were trained under conditions judged more likely to favor the CSs functioning as independent temporal frameworks, while the birds in group B were trained under conditions judged more likely to make the longer-latency CS establish a temporal context within which the shorter-latency CS operated. Subsequently, conditions for both groups were adjusted in ways intended to favor the latter outcome and, hence, a compromise between the two frameworks on displacement trials.

Pretraining

All birds had acquired responding to either the red or X stimulus in a previous autoshaping experiment with a CS duration of 21 s, so, for each subject, one CS was familiar and one novel. In the pretraining phase for this experiment, group A birds were given from one to three sessions of autoshaping with both stimuli presented independently, with reinforcement (3.5 s of hopper access) delivered at CS offset, whether the subject pecked the key or not. These sessions were followed by two sessions in which a peck on the illuminated key was required to obtain reinforcement. Each such session was comprised of 18 trials with the red stimulus and 18 with the X. Group B birds were also given from one to three sessions of autoshaping. Half the trials were with the familiar stimulus, half with the compound. Thus, they sometimes saw the already familiar CS by itself, but they never saw the novel stimulus by itself, only together with the familiar one. For both groups the autoshaping trials in pretraining were fixed 5 s long with a fixed 55-s inter-trial interval (ITI). The pretraining trials that required a response paid off for the first peck. If there was no peck within 10 s of trial onset, the trial ended. The ITI was fixed at 55 s.

Training

In the training procedure, trials were separated by a variable 50–150 s ITI (flat distribution). Reinforcement was 3.5 s access to the food hopper, during which the house light was turned off and a light in the hopper turned on. For both groups, this training phase lasted 30 sessions. The idea behind the training regimes was to have group A repeatedly experience each CS functioning as the sole predictor of reinforcement on trials that both preceded and were intermingled with the trials when the two were presented together (but with asynchronous onsets, that is, in serial compound). In contrast, group B never experienced one of the two

CSs except in serial compound, that is, with its onset always predicted by the earlier onset of the other CS.

In group A, the red CS was the long CS (the FI60 CS). For two of the four birds, this was the initially familiar CS, while for the other two, it was the initially unfamiliar one. The training that followed was designed to make all birds in this group familiar with both CSs. First, there were five sessions in which each stimulus was presented in isolation and reinforced 18 times (18 FI 60 trials with the red CS and 18 FI 15 trials with X CS). This was followed by 25 sessions each with 36 trials, 75% of which were serial compound trials. On these, the key was illuminated red for 45 s, then an X was superposed on the red, and 15 s after that, the key was armed. The first peck on the armed key delivered food and terminated the trial. The remaining 25% of the trials were equally divided between red-alone, with a 60-s arming latency, and X-alone, with a 15-s arming latency. The training conditions for this group were judged likely to favor the establishment of each CS as an independent predictor of food, one (red) predicting it with a latency of 60 s and one (X) predicting it with a latency of 15 s.

For group B, all 36 trials in a session were compound trials, with the second CS coming on 45 s after the first. For all birds, the long CS was the one they were already familiar with (red for two of them, X for the other two), which means that none of the birds in this group ever saw the short CS by itself; they only saw it in compound with the long CS. Group B birds received 30 sessions of training. Note that in group A we counterbalanced for the initial familiarity of the CS but not for stimulus role (the long CS was always red, which was the initially familiar CS for half the birds and the initially unfamiliar CS for the other half), while in group B, we counterbalanced for stimulus role but not initial familiarity (the long CS was red for half the birds and X for the other half, but for all birds, it was the initially familiar one).

Following the training phase, each group passed through a sequence of test conditions. Throughout these test conditions, half of the trials in each session were so-called “peak” trials. On these, the key was never armed. It remained illuminated for a variable interval past the expected arming time. On such trials, responding on most trials brackets the expected time of reinforcement, and the average across trials peaks at approximately the temporal location where the subject expects the key to be armed.

Each test condition was composed of 40 baseline sessions, during which the temporal relation between the long and short CSs was fixed. These baseline sessions were followed by 60 displacement sessions, which were just like baseline sessions, except that on a single

compound peak trial (the "probe" trial), the onset of the short CS was displaced relative to the onset of the long CS. In the first 30 displacement sessions, the onset of the short CS in the probe trial was advanced 30 s; in the second 30 displacement sessions, this onset was retarded by 30 s.

In all the baseline and probe conditions, trials were separated by a variable 50–150 s ITI (drawn from a flat distribution). During reinforcement the house light was turned off and a light in the hopper enclosure turned on.

Condition 1

Group A. The trial structure was the one that prevailed during the training phase–75% compound trials, with the remaining 25% equally divided between red alone and X alone. Half of the trials of each kind were peak trials, on which reinforcement was withheld. On compound peak trials, the compound remained for between 60 and 90 s beyond the expected time of reinforcement. For red-alone and X alone peak trials, the CS persisted for 45–75 s beyond the expected time of reinforcement. On the forward-displacement probe trials, the X CS came on 30 s early—15 s after the red CS; on backward-displacement probe trials, it came on 30 s late—75 s after red onset.

Group B. As in the trainingphase, all trials were compound trials. On peak trials, the compound remained on for a variable time 60–90 s beyond the expected time of reinforcement. On the probe trials during displacement sessions, the second CS was advanced or retarded by 30 s.

Condition 2

The baseline conditions were changed in an attempt to make subjects pay more attention to the longer time interval (the intended framework).

In group A, the long CS (red), when it occurred alone, predicted more food than the short latency CS (X), when it occurred alone—6 s of access versus 3 s. On compound trials, access was randomly either 3 or 6 s in duration. On probe trials, which were always compound peak trials, the onset of the X was advanced or retarded by 30 s, as before.

In group B, the baseline onset asynchrony was shortened from 45 to 30 s, so that, on those probe trials when the onset of the second CS was advanced by 30 s, its onset coincided with that of the first CS.

Condition 3

Only group A went to this condition. Reinforcement on X-alone trials was reduced to the hopper coming up and immediately going back down. Half of the compound trials also received this reduced reinforcement. Thus, when the short CS was presented by itself, no food was actually obtained. Food was only obtained on compound trials, which, one might think, would increase the control exerted by the longer CS, whose onset was more remote in time from the opening of the food hopper.

Results

Figure1 shows the peak trial data from the last 5 of the 40 baseline sessions in condition 1. Response rate is plotted against the time before and after reinforcement, so that the expected time of reinforcement is at 0. The baseline data are in the top four panels (A, B,C, and F). In group A, the red-alone trials show a broad peak centered near the time of reinforcement (Fig. 1A). The X-alone trials (1B) show a much sharper peak. Compound trials (1C) are identical to red-alone trials until the X comes on, 15 s before reinforcement. Thereafter responding on compound trials is the same as responding on X-alone trials. Group B, which had only compound trials, shows a similar pattern (1F), but with considerably less responding in the interval before the second CS comes on.

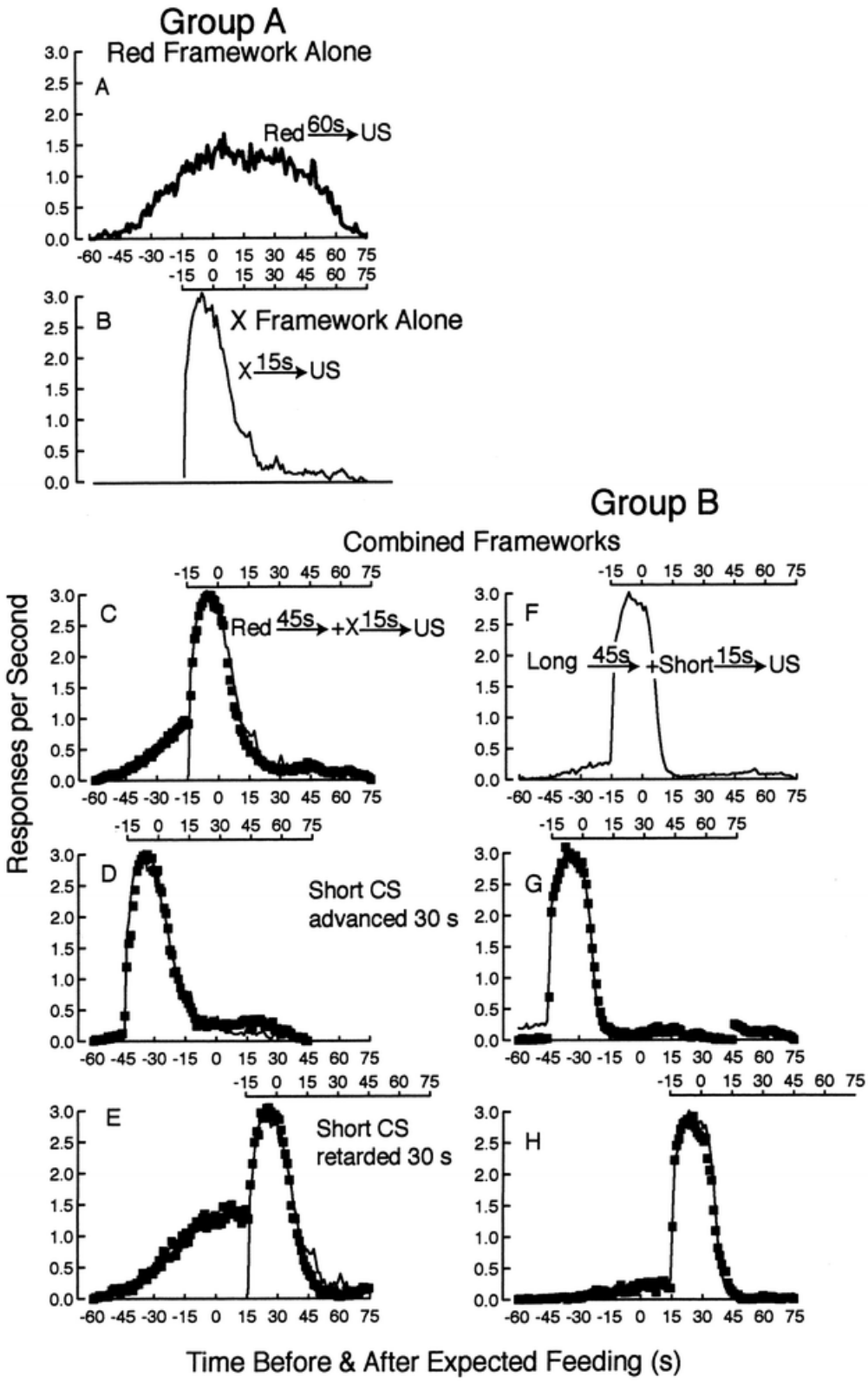

Fig. 1. Average response rates on unreinforced ("peak") trials in condition 1, plotted with the expected time of feeding as the origin (time 0). The panels on the left are for group A; on the right for group B. *A* Trials with red conditioned stimulus (CS) only (expected feeding latency=60 s). *B* Trials with X CS only (expected feeding latency=15 s). *C* Compound trials, with the two temporal frameworks aligned (*filled squares*). The data from the X-only trials are reproduced for reference (*thin curve*). In

the interval after the X comes on, the data from compound trials superpose on the X-only curve. *D* Compound probe trials with the onset of the X CS advanced by 30 s (*filled squares*). The data from the X-only trials are reproduced for reference, shifted to the left along with the X reference frame (*thin curve*). Again, the data from the compound trials superpose on this curve, in the interval after the (unexpectedly early) onset of the X. *E* Compound probe trials with the onset of the X CS retarded by 30 s. The data from the X-only trials are reproduced for reference, shifted to the right along with the X reference frame (*thin curve*). Again, the data from the compound trials superpose on this curve, in the interval after the (unexpectedly late) onset of the X. *F* Compound peak trials for group B, with the two frameworks aligned. For this group, all trials were compound trials; there were no trials with only one of the two CSs. *G* Probe trials with the onset of the short CS advanced by 30 s (*filled squares*). The data from the aligned trials are reproduced for reference, shifted to the left along with the short reference frame (*thin curve*). The data from the probe trials superpose on this curve, in the interval after the (unexpectedly early) onset of the short CS. *H* Probe trials with the onset of the short CS retarded by 30 s. The data from the aligned trials are reproduced for reference, shifted to the right along with the short reference frame (*thin curve*). The data from probe trials superpose on this curve, in the interval after the (unexpectedly late) onset of the short CS

The results from the 30 displacement trials of each kind are plotted in the bottom four panels of Fig. 1. For reference, the results from the relevant trials of the baseline condition are also plotted in these panels, displaced by the same amount as the onset of the short CS, in other words, in the same location relative to this CS. In each case, the data from the displacement trials during the interval after the displaced short CS came on fall on top of the displaced reference data. In other words, the peak response tendency on displacement trials is at the location predicted by the short CS; there is no evidence of a compromise between this location and the location predicted by the long CS. Nor is there evidence for the summation of response tendencies to the temporal elements (successive portions) of the two CSs. Once the short CS has come on, responding is what would be expected if the long CS were no longer present. When the onset of the short CS was displaced closer to the onset of the long CS, subjects ceased responding when the US location it predicted was passed. When that location was passed, they did not respond to the middle portion of the long CS (panel D of Fig. 1); whereas, on trials where the short CS came on later or not at all, they responded strongly to this portion (panels A and E of Fig. 1).

Figure 2 shows the results from the second condition, plotted in the same way as in Fig. 1. Increasing the amount of reinforcement of the red (=long) CS in group A increased the

peak rate of responding on red-alone trials but did not change its timing (Fig. 2A). Oddly, the peak rate was also increased on X-alone trials, despite the (modest) decrease in the amount of reinforcement on these trials. On compound trials, the peak rate was lower than the peak rate on X-alone trials, but the profile during the interval after the X came on was the same as on X-alone trials. Again, the results from the 30 displacement trials of each kind are plotted in the bottom four panels, together with displaced reference data from the baseline sessions, and again the peak is at the location predicted by the short CS. There is no evidence of compromise, even on trials where the onset of the short CS coincided with the onset of the long CS (Fig. 2G). Nor is there evidence of summation: when the temporal location of the US predicted by the onset of the displaced short CS was passed, responding ceased, even though subjects responded strongly to that portion of the long CS on trials where the short CS had not yet come on (compare panel D of Fig. 2 with panels A and E).

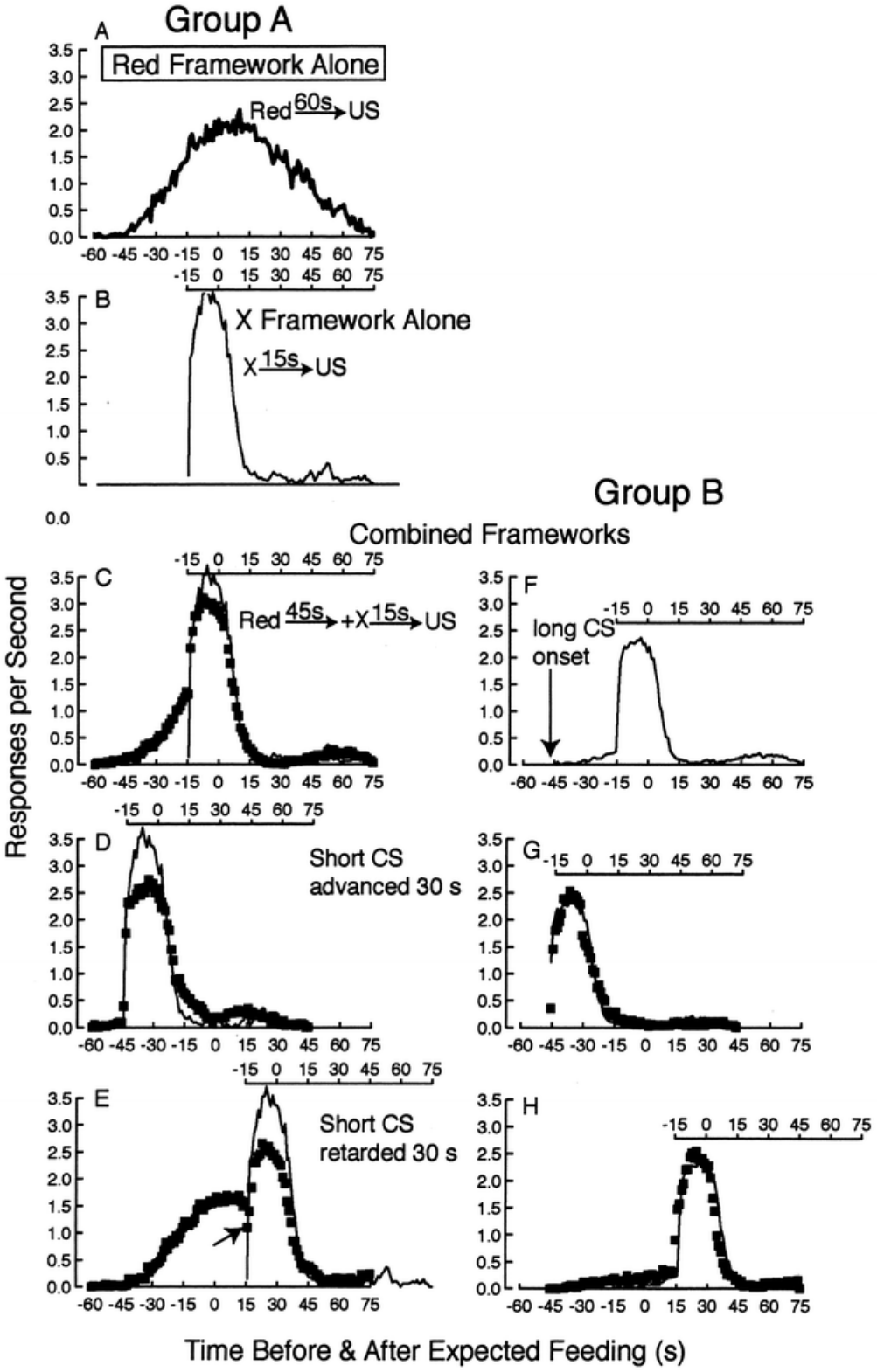

Fig. 2. Average response rates on unreinforced ("peak") trials in condition 2 plotted with the expected time of feeding as the origin (time 0). The panels on the left are for group A; on the right, for group B. *A* Trials with red CS only (expected feeding latency=60 s). *B* Trials with X CS only (expected feeding latency=15 s). *C* Compound trials, with the two temporal frameworks aligned (*filled squares*). The data from the X-only trials are reproduced for reference (*thin curve*). In the interval after the X comes on, the data from compound trials are lower than the X-only curve, but they peak at the same

location. *D* Compound probe trials with the onset of the X CS advanced by 30 s (*filled squares*). The data from the X-only trials are reproduced for reference, shifted to the left along with the X reference frame (*thin curve*). The data from the probe trials peak at the same location relative to the X framework; there is no effect of the red framework on the location of the peak. *E* Compound probe trials with the onset of the X CS retarded by 30 s. The data from the X-only trials are reproduced for reference, shifted to the right along with the X reference frame (*thin curve*). The data from the probe trials peak at same location relative to the X-framework; there is no effect of the red-framework on the location of the peak. *F* Compound peak trials for group B, with the two frameworks aligned. Note that the long CS onset now occurs 45 s before the expected feeding time (instead of 60 s). **G.** Probe trials with the onset of the short CS advanced by 30 s, so that its onset now coincides with that of the long CS (*filled squares*). The data from the aligned trials are reproduced for reference, shifted to the left along with the short-CS reference frame (*thin curve*). The data from the probe trials superpose on this curve, in the interval after the (unexpectedly early) onset of the short CS. *H* Probe trials with the onset of the short CS retarded by 30 s. The data from the aligned trials are reproduced for reference, shifted to the right along with the short reference frame (*thin curve*). The data from probe trials superpose on this curve, in the interval after the (unexpectedly late) onset of the short CS

Figure 3 shows the results from the third condition, where X alone predicted only the raising and lowering of the hopper, with no opportunity to eat. The effect of this on peak responding on X alone trials is readily apparent (Fig. 3B), but once again, the location of the peak on displacement trials was entirely determined by the short CS, with no evidence of a compromise. When the short CS came on, it took control of the timing of the conditioned response. Immediately after its onset, responding was considerably reduced relative to moments earlier when only the long CS was present (arrows in panels C and E of Fig. 3). This demonstrates once again that conditioned responding was determined by the location of the proximal landmark; it was not the sum of response tendencies to different elements (portions) of the two CSs.

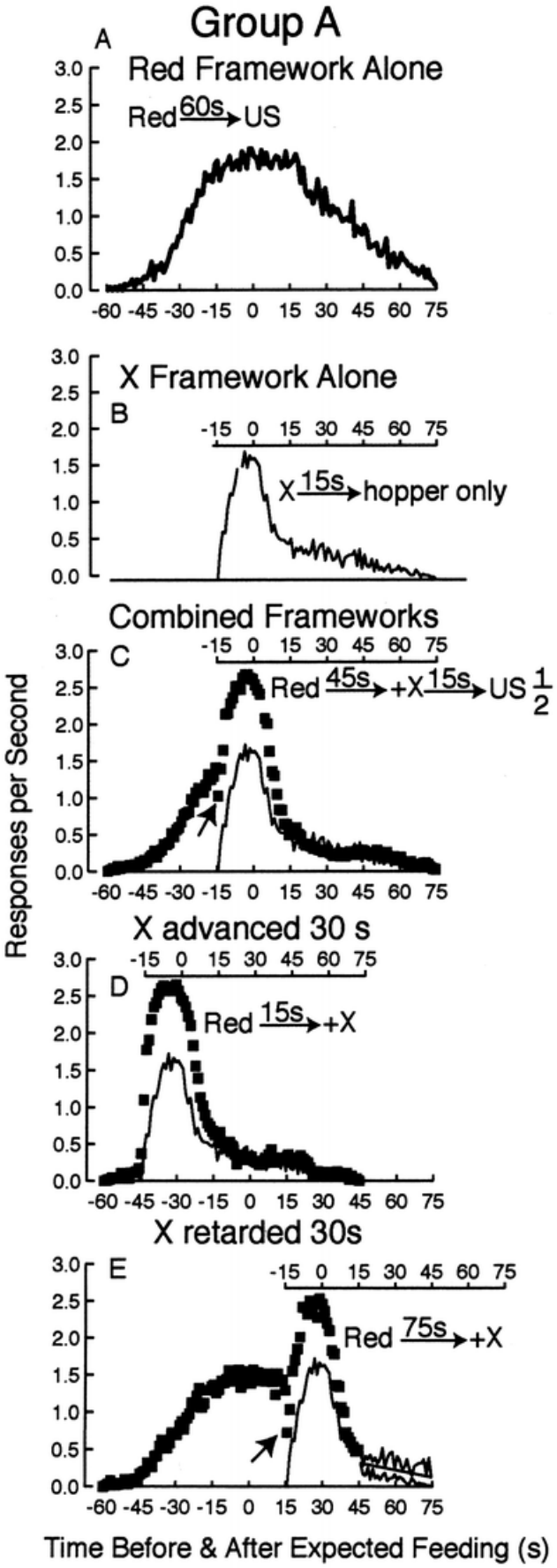

Fig. 3. Average response rates on unreinforced ("peak") trials in condition 3 plotted with the expected time of feeding as the origin (time 0). *A* Trials with red CS only (expected feeding latency=60 s). *B*

Trials with X CS only (expected time to the raising and lowering of the hopper=15 s). *C* Compound Trials, with the two temporal frameworks aligned (*filled squares*). The data from the X-only trials are reproduced for reference (*thin curve*). *D* Compound probe trials with the onset of the X CS advanced by 30 s (*filled squares*). The data from the X-only trials are reproduced for reference, shifted to the left along with the X reference frame (*thin curve*). *E* Compound probe trials with the onset of the X CS retarded by 30 s. The data from the X-only trials are reproduced for reference, shifted to the right along with the X reference frame (*thin curve*)

Discussion

Our data show that when the temporal location of a US is indicated by compounded CSs with asynchronous onsets, the two CSs do not establish potentially competing temporal frameworks. When the short CS is displaced relative to the long CS, it entirely determines the location of the peak in US expectation; there is no evidence of a location at a compromise between the location signaled by the long CS and the location signaled by the short CS. Nor do response tendencies to portions of the two CS sum; the timing of conditioned responding is governed solely by the location of the more proximal temporal landmark.

That the more proximal landmark should control the timing of the response is not surprising given the well-established scalar variability in remembered temporal intervals (Gibbon 1977; Killeen and Weiss 1987; Gallistel and Gibbon 2000). Closer landmarks are better landmarks from an information-theoretic perspective (Shannon 1948), because the closer a warning is to the event, the greater the amount by which it reduces the subject's uncertainty about when that event will occur (Gallistel 2002). This, however, does not explain why there is no effect of the long CS on the location of the peak when the long and short CSs signal different US locations. This lack of any measurable effect suggests that under these circumstances, the principal function of the long CS is to signal the location of the onset of the short CS. It sets the occasion for the anticipation of the US, but the countdown to the US, so to speak, does not begin until the onset of the short CS—the last warning.

Consistent with this suggestion is the contrast between group A and group B in the amount of responding to the long CS in the interval prior to the onset of the short CS. For group A, it was uncertain on any given trial whether there would be a short CS. Not surprisingly, these subjects responded to the red (=long) CS on compound trials exactly as they did on red-alone trials, up until the X came on. For group B, there was always the onset of a short CS at a

predictable latency after the onset of the long CS. These subjects showed a much weaker response to the long CS in the interval prior to the onset of the short CS. If the long CS functioned mostly in an occasion-setting capacity, this would be expected. We note in this connection, that an occasion-setting like effect may be observed in the spatial domain, as well. The landmark nearest the target location controls the locus of a bee's search only if the background panorama is the same as during training (Collett et al. 2002). This background panorama seems to establish a spatial context within which the local landmark becomes behaviorally effective, just as an occasion-setter establishes a temporal context, within which a proximal temporal landmark becomes behaviorally effective.

On the other hand, one could argue that because there was some responding to the long CS in group B, it was not an occasion-setter, or, at least not purely an occasion-setter. Be that as it may, the finding that the timing of responding is controlled entirely by the onset of the proximal CS is consistent with the finding that the conditioned response in a serial-compound (occasion-setting) paradigm tends to be a response specifically to the proximal CS, rather than to the CS with the more remote onset, or to the compound (Holland 1983, 1986).

These results contrast with the earlier results in which there were compromises between the location predicted by the circadian temporal framework and the location predicted by a (very long) CS. Circadian and interval timing mechanisms establish potentially conflicting frameworks for estimating the time of reinforcement, while concurrent interval timing cues with asynchronous onset do not. When the circadian and interval timing frameworks are displaced relative to one another, the temporal location at which the expectation of reinforcement is maximal is a compromise. When a short-latency interval-timing cue is displaced relative to a concurrent long-latency cue, the temporal location at which the expectation of reinforcement is maximal is not a compromise; it is determined entirely by the CS whose onset is closer to the time of reinforcement.

From an information theoretic standpoint, this means that response timing is governed by the stimulus that maximally reduces the subject's uncertainty about the temporal location of reinforcement. That may be why proximity prevails.

Acknowledgements Grant MH14649 from the National Institute of Health (USA) to John Gibbon supported this research. The research was conducted in accord with the prior approval of the Institutional Review Board of the New York State Psychiatric Institute and with all

applicable animal care and welfare laws and regulations. The helpful comments and suggestions of Peter Balsam are gratefully acknowledged.

References

Cheng K (1989) The vector sum model of pigeon landmark use. J Exp Psychol: Anim Behav Process15:366–375

Collett M, Harland D, Collett TS (2002) The use of landmarks and panoramic context in the performance of local vectors by navigating bees. J Exp Biol 205:807–814

Gallistel CR (1990) The organization of learning. Bradford Books/MIT Press, Cambridge, Mass

Gallistel CR (2002) Frequency, contingency and the information processing theory of conditioning. Etc. frequency processing and cognition. In: Sedelmeier P, Betsch T (eds) , Oxford University Press, Oxford pp 153–171

Gallistel CR, Gibbon J (2000) Time, rate and conditioning. Psychol Rev 107:289–344

Gibbon J (1977) Scalar expectancy theory and Weber's Law in animal timing. Psychol Rev 84:279–335

Gibbon J, Fairhurst S, Goldberg B (1997) Cooperation, conflict and compromise between circadian and interval clocks in pigeons. In: Bradshaw ECM, Szabadi EE (eds) Time and behaviour: psychological and neurobehavioural analyses. Elsevier, Amsterdam, pp 329–384

Holland PC (1983) Occasion-setting in Pavlovian feature positive discriminations. In: Commons ML, Herrnstein RJ, Wagner AR (eds) Quantitative analyses of behavior: discrimination processes. Ballinger, New York, pp 183–206

Holland PC (1986) Temporal determinants of occasion setting in feature positive discriminations. Anim Learn Behav 14:11–120

Holland PC, Hamlin PA, Parsons JP (1997) Temporal specificity in serial feature-positive discrimination learning. J Exp Psychol: Anim Behav Process 23:95–109

Honig WK (1981) Working memory and the temporal map. Information processing in animals: memory mechanisms. In: Spear NE, Miller RR (eds) Erlbaum, Hillsdale, NJ, pp 167–197

Killeen PR, Weiss NA (1987) Optimal timing and the Weber function. Psychol Rev 94:455–468

Miller RR, Barnet RC (1993) The role of time in elementary associations. Curr Dir Psychol Sci 2:106–111

Mistlberger RE (1994) Circadian food-anticipatory activity: formal models and physiological mechanisms. Neurosci Biobehav Rev 18:171–195

Savastano HI, Miller RR (1998) Time as content in Pavlovian conditioning. Behav Proc 44:147–162

Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J, 27:379–423, 623–656

Srinivasan MV, Zhang SW, Bidwell NJ (1997) Visually mediated odometry in honeybees navigation en route to the goal: visual flight control and odometery. J Exp Biol 200: 2513–2522