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EFFECTS OF FOOD-PELLET SIZE ON RATE, LATENCY, AND TOPOGRAPHY OF AUTOSHAPED KEY PECKS AND GAPES IN PIGEONS

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Four pigeons responded under autoshaping contingencies in which different conditional stimuli (red or green keylights) were associated with unconditional stimuli of different magnitudes (large or small food pellets) over successive trials within a session. Both topography (beak opening or gape) and strength (rates and latencies of key pecks and gapes) of responding during the conditional stimuli depended on the magnitude of the correlated unconditional stimulus. Key-peck and gape rates were higher and latencies were shorter in large-pellet trials than in small-pellet trials. Gape amplitudes varied directly with pellet size, although conditional and unconditional gapes were larger than either pellet. These findings were replicated when the key colors were presented either on one or two keys and after reversals of the color-size correlations. Because the unconditional stimulus was varied through pellet size, magnitude was not confounded with food-access duration or quality. These results demonstrate the effects of the magnitude of the unconditional stimulus, in that rates and latencies of both key pecks (which are directed movements toward the key) and gapes (which are independent of the bird's position and key properties) varied with pellet size. Gape measures were unique in that two dimensions (response strength and topography) of a single response class varied simultaneously with magnitude.

Key words: autoshaping, response rate, latency, topography, unconditional stimulus, pellet size, key peck, gape, pigeon

Studies of autoshaping in pigeons have purported to show a number of functional relationships between the properties of an unconditional stimulus (US) and several dimensions of the resulting conditional response (CR). There is reasonable evidence that US magnitude (measured as number of pellets or feeder-access duration) controls both rate and latency of the CR (Balsam, Brownstein, & Shull, 1978; O'Connell & Rashotte, 1982; Perkins et al., 1975). There is also evidence that US quality (e.g., food and water comparisons) controls CR topography (Allan & Zeigler, 1994; Jenkins & Moore, 1973; LaMon & Zeigler, 1984, 1988). Both findings are still uncertain, however, because the usual ways of manipulating the US dimensions confound several possible independent variables. It is especially difficult to avoid these confounding effects when several response dimensions are to be assessed simultaneously. In what follows, we discuss the confounding effects inherent in several types of studies. We then propose a procedure for simultaneously measuring the functional relationships between pellet size (US magnitude) and CR rate, latency, and topography.

Although a number of studies have reported that US magnitude controls CR rate and latency, it has not been easy to specify all the relevant dimensions of magnitude (e.g., weight, calories, size, number, and duration). The problem is that the methods used to control magnitude may cause variations in other crucial aspects of the US. When magnitude is controlled by feeder-access time (Balsam et al., 1978) or by the number of standard-sized pellets per US presentation (O'Connell & Rashotte, 1982), each US presentation elicits several unconditional eating responses (URs) that are proportional in number to US magnitude. Both US duration and the number of URs are therefore confounded with magnitude.

Another confounding effect exists in the usual procedures for investigating US effects on CR topography. For example, LaMon and Zeigler (1984) showed the effect of US size (various seed types with differing diameters) on conditional beak opening (gape). Because size was confounded with grain type, however,

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it is uncertain which feature controlled gape size. The quality of the US has also been shown to have independent effects on response rates (Miller, 1976; cf. Killeen, Cate, & Tran, 1993). Therefore, this manipulation is unsuitable for assessing the effects of US size on CR rates.

Other studies have demonstrated that CR topographies are different for water USs and food USs (Allan & Zeigler, 1994; Jenkins & Moore, 1973; LaMon & Zeigler, 1984, 1988), but it would be difficult to show that CR rates are controlled by US quality in the same way. First, it is known that deprivation levels affect response rates (cf. Boakes, Poli, Lockwood, & Goodall, 1978). It is not clear, however, how to equate water and food deprivation levels. Differences in response rates may thus reflect differences in deprivation rather than in quality of the US. Second, rate measures require specification of a discrete response unit (e.g., key-switch closure), but such units are not easily defined for topography measures such as gape. For example, Allan and Zeigler (1994) provided a good operational definition for the simple occurrence of gape responses, but it would be impossible to compare the response rates associated with the two USs. The difficulty is that the two rates would be based on different measuring standards. The number of gapes during drinking is a function of the duration of a single water presentation, whereas the number of gapes during eating depends on the number of pellets presented. Third, because food and water control different CR topographies, key-switch closures themselves could be confounded with topography. For example, rapid and rhythmic gapes without pecks (neck movements), which are typical for drinking, could operate the switch at a high rate if the beak movements occur at the trigger point of the switch; they could also produce low response rates if the gapes occur while the key remains either pressed or unpressed. Key properties and response topography might therefore interact unpredictably to produce meaningless peck-rate measures.

It is sometimes difficult, too, to interpret studies that vary US properties between subjects or between sessions (e.g., Allan & Zeigler, 1994; LaMon & Zeigler, 1984, 1988). In particular, response topographies that appear to reflect some US property might be the result of simple response generalization from consummatory responses (whose form is specific to the only US type used in a session). Differences in CR topography, therefore, may not depend on the association of the conditional stimulus (CS) with the US (cf. Jenkins & Moore, 1973).

Despite these difficulties, it remains desirable to measure CR rate, latency, and topography simultaneously. First, gape measures not only allow assessment of topography, but, because they are independent of key-switch closures, they also provide alternative measures of response rate and latency that are not affected by specific key properties (e.g., throw and force requirements). Second, because gapes and pecks might be controlled by different contingencies, assessment of both might reveal the control of different components of the CR. Key-peck measures, for example, depend on head transport toward the key to trigger the switch. Gapes, on the other hand, can be measured independent of any spatial relation to the conditioning chamber and its components. A key peck is therefore always associated with an approach to the CS, and this feature may add an inadvertent contingency between the response (peck, head transport) and the reinforcer. Gapes are independent of any such contingency.

In this study we assessed the effects of US magnitude on CR rate, latency, and topography within sessions and within subjects. The magnitude of the US was varied by using different-sized pellets of identical composition. Thus, the duration and quality of the US, as well as the number of consummatory responses per US presentation, remained constant. The basic response topography (eating) also remained unchanged and so avoided the problem of identifying comparable response units. Rates and latencies of both gapes and pecks were recorded. Gape measures had the advantage over peck measures in that they were not affected by the specific key properties and did not depend on approach to CS. Gapes (specifically gape amplitudes) were also used to measure the relation between pellet size and the topographies of the CR and UR with the same metric. Four conditions were arranged. The correlation between the CS (color) and the US (pellet size) was reversed twice to demonstrate, during reacquisition, the robustness of the pellet-size effects. Furthermore, the CSs that signaled pellet size were presented on either one or two keys to assess whether spatial separation of the two CSs would increase response differentiation.

METHOD

Subjects

Four experimentally naive White Carneau pigeons were housed in individual cages under a 12:12 hr dark/light cycle, with water and grit always available. They were maintained at 80% of their free-feeding weights by food obtained in experimental sessions and by supplementary rations in their cages.

Apparatus

The experiment was carried out in a sound-attenuating enclosure with additional sound masking by white noise. The enclosure contained an operant conditioning chamber (31.5 cm long, 34 cm wide, 35.5 cm high). All walls (6 mm thick) were of clear acrylic except for the gray intelligence panel (front) equipped with three pigeon keys (2.5 cm diameter) mounted 20 cm above the metal grid floor with a center-to-center distance of 7.5 cm. The keys could be transilluminated with red, green, or white 1-W bulbs. A minimum force of 0.18 N was necessary to trigger the key switches. To minimize possible contacts between the beak-mounted transducer or magnet (see below) and the edge of the key aperture, a clear acrylic insert (6 mm thick) was glued to the key surface, raising it to the level of the intelligence panel. The center key was taped over to render it inoperative. For pretraining and the first two experimental conditions the chamber was divided in half lengthwise so that only the right key was available. The divider, a clear acrylic sheet, extended from the floor to the ceiling and from the back wall to the intelligence panel. The houselight consisted of two ceiling-mounted 2.8-W clear bulbs that were lit at all times except during food presentations, during which the hopper was illuminated by a 2.8-W clear bulb. Spherical Bioserv food pellets (4.9 mm or 9.2 mm diameter, 75 mg or 500 mg) were delivered by a universal feeder (Davis Scientific Instruments, Model 310) that was preloaded at the start of each session according to a predetermined quasi-random sequence. Pellets were delivered through a tube (13 mm) onto a raised watchglass (5 cm diameter) mounted on a solenoid-operated modified dipper mechanism. When raised, the watchglass served as the bottom of a round receptacle (4.8 cm diameter) cut out of an acrylic block (18 mm thick). The pigeons could reach the pellets on the watchglass through an aperture (9 cm by 10 cm). At the end of the reinforcement period, the watchglass was lowered to dispose of unconsumed pellets. Scheduling of experimental events, data collection, and data analysis were performed by a Macintosh IIci® computer, an I/O interface card with 12-bit analog-to-digital converter (National Instruments, Model Lab-NB®), and customized software (LabVIEW®).

Recording of beak opening (gape). To obtain measures of response topography, the distance between the tips of the lower and upper beaks (gape) was continuously recorded. This was done by gluing a small neodymium magnet to the pigeon's lower beak and a magnetosensitive Hall-effect microchip (Allegro Electronics, Model UGN3503U) to the upper beak (Deich, Allan, & Zeigler, 1988; Deich, Houben, Allan, & Zeigler, 1985). The fine wires from the chip were glued to the back of the pigeon's head to avoid entanglement and then were plugged into a ceiling-mounted phone jack. The chip's continuous voltage output, which is proportional to the beak opening, was digitized with the analog-to-digital converter and was recorded at a 1-ms sampling rate. (The key-switch state, open or closed, was recorded in a similar manner to preserve information on the temporal relations between gape and pecks.) The gape-monitoring system was calibrated before and after each session by placing a tapered aluminum rod (with 2-mm diameter gradations) between the beak tips to produce gapes increasing from 2 to 20 mm in 2-mm steps, and by recording the corresponding digital values. For subsequent data analysis, an exponential curve was fit to the points defined by these pairs of analog-digital values. The reversal function describing this curve was then used to convert any observed digital values to their corresponding analog values (in millimeters). Figure 1 is a sample of the form of data collected for each trial from which mea-

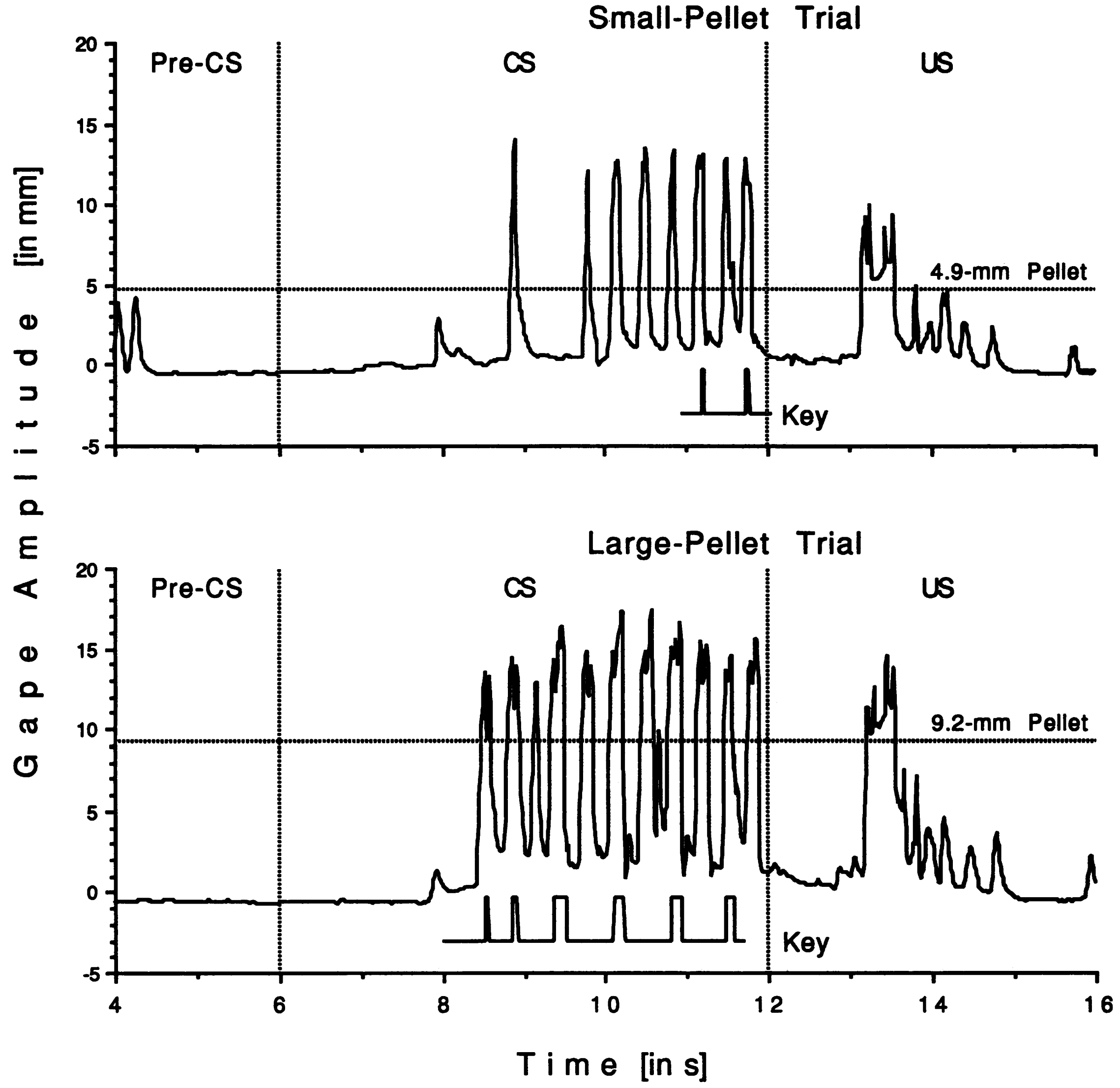

Fig. 1. Beak openings (gapes) and key pecks depicted in a partial sample record (2 s of pre-CS, 6 s of CS, and 4 s of US) from 1 pigeon and from one trial with a 4.9-mm pellet (top graph) and a 9.2-mm pellet (bottom graph) as US, as indicated by dotted horizontal lines. Dotted vertical lines indicate transitions from pre-CS to CS to US. Data are from P1 from Trials 31 and 36 of the last session of the two-key reversal condition. The two traces in the middle panel of each graph (CS period) share a common time base (abscissa, in seconds). One represents gape amplitudes (ordinate, in millimeters). The other, labeled *Key*, represents pecks defined by key-switch closures (high when switch closed, low when switch open). The US records (right panels) show gape variations during eating.

sures of key-peck and gape rate, latency, and topography could be derived.

Procedure

Pretraining. After all pigeons reliably ate a mixture of both 4.9-mm and 9.2-mm pellets presented together on the raised watchglass, they were trained within two or three sessions to eat single pellets (large and small in random order) within 3 s of feeder operation. Each single-pellet presentation was preceded by a 3-s illumination of a white keylight.

Experimental conditions. The effect of pellet size on response rate, latency, and topography was assessed by recording key-switch closures and beak openings under autoshaping contingencies (P. Brown & Jenkins, 1968). A successive discrimination procedure was used in which two keylight colors signaled the two pellet sizes. In each trial, illumination of a red or green keylight (CS) was followed by the response-independent delivery of a 4.9-mm pellet (small-pellet trial) or a 9.2-mm pellet (large-pellet trial). Small-pellet and large-pellet trials alternated randomly with two restrictions (Jenkins, 1965). First, the same size was not presented in more than three consecutive trials. Second, an equal number of both sizes was delivered in each session. Upon delivery of a pellet, the hopper was illuminated for 6 s (US period). Trials were separated by a variable intertrial interval (ITI) lasting a mean of 60 s, based on a variable-interval 54-s schedule (Fleshler & Hoffman, 1962) with a 6-s constant added to each interval. This allowed sampling of key pecks and gapes for 6 s prior to CS presentation (pre-CS) and throughout the 6-s CS and US periods. Each session ended after 36 trials.

The four experimental conditions, in order, were as follows: (a) one-key baseline (15 sessions): The chamber divider was inserted and only the right key was available. For P1 and P3 a red keylight signaled the delivery of a small pellet; green signaled the delivery of a large pellet. The opposite color-size assignment was used for P2 and P4. (b) One-key reversal (10 sessions): For all pigeons the color-size correlation was the reverse of that in the preceding condition. (c) Two-key baseline (15 sessions): The chamber divider was removed to make both keys available. For all pigeons the green keylight was always presented on the right and the red keylight on the left, but the color-size correlations remained the same as in the preceding condition. (d) Two-key reversal (10 sessions): The color-size correlation was reversed for all pigeons, but the color-position correlation remained unchanged.

Definition of the Gape Response Measures

Because gape was recorded as a continuous variable over time, it was necessary to define a discrete gape response. A gape response was defined as any beak opening whose amplitude first exceeded 4.5 mm and then, after a minimum of 5 ms, fell below this criterion level. The gape amplitude for that response was defined as its maximum opening. The 4.5-mm criterion was selected because visual inspection of the data indicated that gapes during the pre-CS and CS periods fell into two distinct categories, one with amplitudes below 4.5 mm on average (subcriterion gapes) and the other above that level (supercriterion gapes). Subcriterion gapes occurred during both the pre-CS and CS periods, and in both small- and large-pellet trials (see Figure 1, gapes at 4 s and 8 s). Supercriterion gapes occurred during the CS only, were often associated with key pecks, and were smaller and less frequent during small-pellet than large-pellet CSs (Figure 1, middle panels). Because subcriterion gapes appeared to be nondifferential and random, they were excluded from the analysis of CRs (cf. Allan & Zeigler, 1994).

To justify this exclusion, it had to be shown that small-pellet trials produced as many gapes with amplitudes below 4.5 mm as large-pellet trials did (so that the criterion would not differentially exclude gapes from small-pellet trials). This required the use of a lowered (2-mm) criterion to include subcriterion gapes. Applying the 2-mm criterion also necessitated a minor modification of the gape definition (for this analysis only). As seen in Figure 1, the absolute value of beak openings between gape responses did not always drop below 2 mm, which, when applying an absolute 2-mm criterion, would incorrectly disqualify these gapes as individual responses. What should in fact count as responses are those gapes, including those with small amplitudes, that exceed, by the specified criterion, the beak "resting" position that occurs before the response. Accordingly, the 2-mm criterion was applied to beak resting positions rather than to absolute gape levels. Beak resting position was defined as the most frequent gape level (in millimeters) during the CS. (Because a zero value was assumed when the beak tips were perfectly congruous, the resting position value could be negative when the maxilla protruded over the mandible, which is possible with pigeons' movable upper and lower jaws.) The 2-mm analysis showed that small-pellet trials produced as many gapes with amplitudes below 4.5 mm as large-pellet trials did, so that the 4.5-mm criterion did not differentially exclude gapes from small-pellet trials. In fact, inclusion of subcriterion gapes would underrepresent the extent of differ-

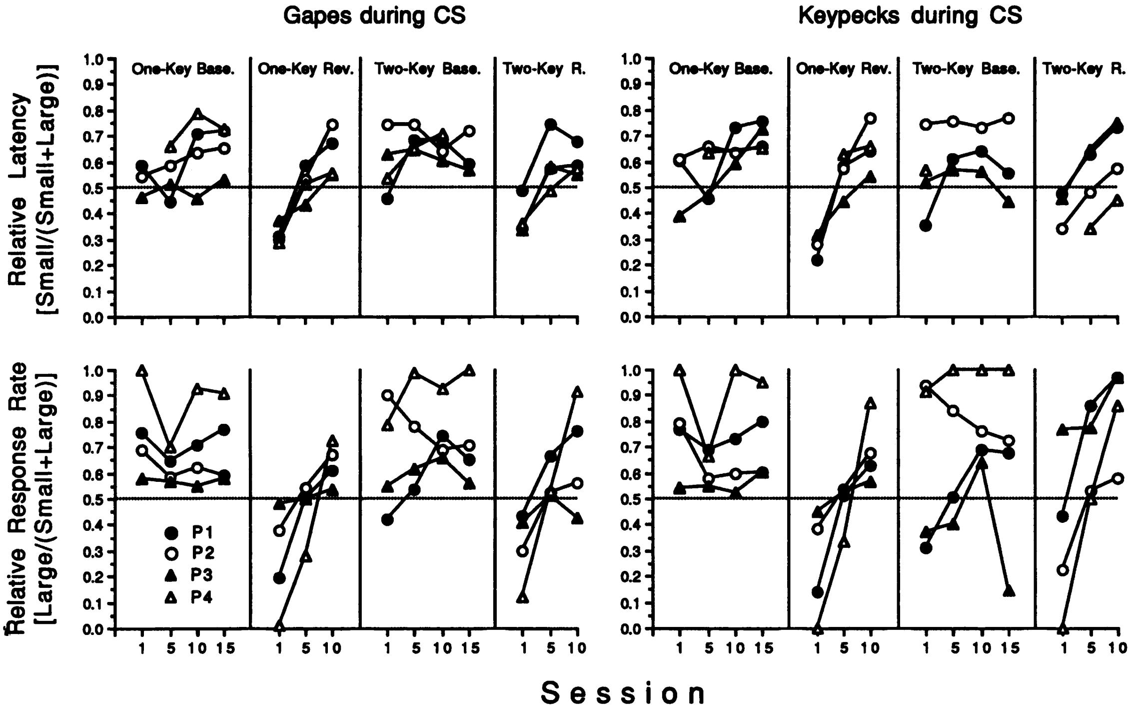

Fig. 2. Measures of relative latencies and response rates (top and bottom graphs) based on gapes and key pecks (left and right graphs) for each of the 4 pigeons and four conditions obtained in the first and every fifth session (for exceptions, see footnotes to the Appendix). The dotted horizontal lines indicate indifference; that is, response rates and latencies at that level were the same for small-pellet and large-pellet trials.

ential responding. Consequently, all gape measures were based on the 4.5-mm criterion. Because beak resting position was criterion independent, it represents an alternative gape measure.

RESULTS

The results will be presented in two sections: one describing the effect of pellet size on rates and latencies of both key pecks and gapes (4.5-mm criterion; see Method section), and the other describing the effect of pellet size on gape amplitude. In order to indicate the relative effect of large pellets versus small pellets on the various response dimensions, all data will be presented as relative measures (either proportions or difference scores). Furthermore, all measures will be presented such that increases in value correspond to greater control by the large pellet than the small. Relative response rates (which are directly related to US magnitude) were calculated as the total responses during large-pellet CSs divided by the sum of the responses on large- and small-pellet trials. Relative latencies (which are inversely related to US magnitude) were calculated as the mean latency during small-pellet CSs divided by the sum of the mean latencies during small- and large-pellet trials. Differences in gape magnitude (which are directly related to US magnitude) were calculated as the mean gape amplitude on large-pellet trials minus the mean gape amplitude on small-pellet trials. The absolute values for all measures are provided in the Appendix.

Response Rates and Latencies

Figure 2 shows relative response latencies and relative response rates for both gapes and key pecks during the CS, plotted for the first and every fifth session of each of the four conditions. Gape latency was defined as the time between the CS onset and the point at which the first gape during a CS exceeded 4.5 mm in amplitude. Key-peck latency was defined as the time between the CS onset and the first switch closure during a CS. Trials without responses (estimated to be fewer than 5% of all trials) were not included in the latency analysis. To the extent that pellet size exerted control over response strength, the later sessions of each condition should produce values above .5, indicating that large-pellet trials produced higher response rates and shorter latencies than small-pellet trials did. The first one or two data points in each panel should reflect the conditions prevailing in the previous condition (for the second and fourth conditions, below .5, and for the third condition, above .5). Early sessions in the first condition were expected to reflect behavior that was not yet differentiated with respect to US magnitude (therefore at approximately .5). In general, these predictions were confirmed, in that response rates became higher and latencies shorter during large-pellet trials relative to small-pellet trials. However, deviations from the predictions occurred in that most measures from the very first sessions were above the .5 level, perhaps because pellet size affected the response measures within a few trials. P1 and P3 produced anomalous results in several sessions of the two-key baseline condition. In the last session of the last condition, P3 produced an anomalous gape-rate proportion, as did P4 for peck latency. Overall, as can be verified in the Appendix, absolute key-peck rates were lower than absolute gape rates. Therefore, small changes in allocation of a few pecks to small- or large-pellet CSs could produce a large change in the proportional measure. This is perhaps why proportions based on key pecks varied over a wider range than did proportions based on gapes. Also, because of low response rates and because latencies were undefined if no response occurred, the following measures could not be obtained for P4: key-peck and gape latencies in the first session of the first condition, key-peck latencies in the first session of the second and fourth conditions, and key-peck latencies in the last three sessions of the third condition.

Response Topography

Figure 3 depicts three topography measures as a function of pellet size for each pigeon and for the first and every fifth sessions of each of the four conditions. Shown are beak resting positions during the CS and amplitudes of the first gapes during the CS and the US. To minimize possible distortion of the response topographies by contact with the key, only the first gape during the CS was included in the analysis, because it usually occurred prior to key contact. (However, an analysis including all gapes during the CS produced similar results.) Similarly, analysis of gapes during the US period was limited to gape values (peak amplitude) for the first beak opening prior to contact with the pellet. The data were calculated as follows: First, for each measure, pigeon, and session, a mean was obtained separately for small-pellet and large-pellet trials. Then numbers from small-pellet trials were subtracted from those of large-pellet trials to obtain difference scores. Positive scores indicate that gapes during the large-pellet CS were larger than gapes during the small-pellet CS, whereas negative numbers indicate the opposite. Thus, control by pellet size is reflected in Figure 3 (as in Figure 2) by increasing values (lines with positive slope) in the first, second, and fourth conditions. (The expected slope in the third condition is zero assuming that the behavior was stable at the end of the previous condition.) In general, gape amplitudes and beak resting positions were larger in large-pellet trials, but there were some discrepancies. For both the third condition and the last session of the previous condition, P2 produced bigger differences in resting positions than other birds did. Gape amplitudes during the CS yielded a wider range of difference scores (note the ordinates of Figure 3) and were more variable than beak resting position measures. The data of P4 were particularly variable, perhaps because its scores were based on means with only few individual observations (low response rates) that rendered the difference scores less stable. For P4, scores for the first session of the first condition and the last session of the third condition could not be calculated, because gapes were observed only for large-pellet trials.

As with conditional gapes, the magnitude of unconditional gapes increased over the first, second, and fourth conditions. (However, small pellets never caused bigger gapes than large pellets, indicated by positive difference scores for all sessions.) The change in size of unconditional gapes was unexpected because these gapes were presumed to be

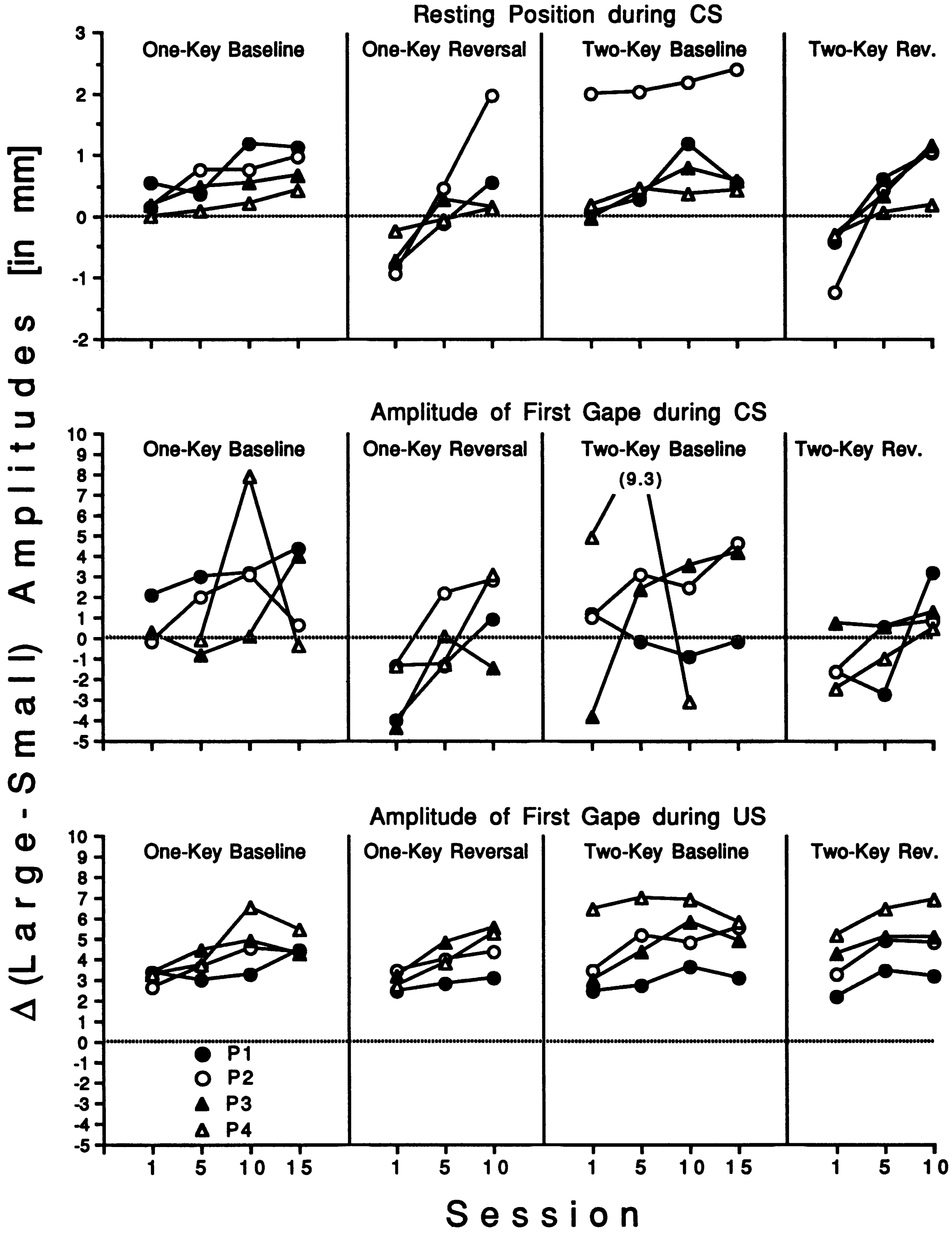

Fig. 3. Three measures of response topography for each pigeon and for the first and every fifth session of each condition (for exceptions, see footnotes to the Appendix), expressed as difference scores from large-pellet and small-pellet trials. The top graph shows the beak resting position during the CS period, the middle graph represents the

controlled directly by pellet size and were independent of CS-US contingencies.

For conditional and unconditional gapes, amplitudes in both small- and large-pellet trials were considerably larger than ("overshot") the diameter of either pellet (Appendix; see also Figure 1). The extent of overshoot was up to 12 mm for conditional gapes and up to 6 mm for unconditional gapes.

Two of three additional measures varied in an orderly way with US magnitude. First, gape rise times (the elapsed time between CR onset, when the gape exceeded the 4.5-mm criterion, and the time when the gape reached its maximum peak) were longer for large-pellet trials than for small-pellet trials. Second, the area delimited by beak resting positions and the amplitude-time functions of individual gapes (estimated by partial integrals across time) were greater for large-pellet trials than for small-pellet trials. The proportion of gapes accompanied by a peck, however, did not vary with pellet size.

DISCUSSION

Key-peck and gape rates, key-peck and gape latencies, gape amplitudes, and beak resting positions during food-associated CSs varied with US magnitude (pellet size). These results extend the conditions over which US properties are known to control CR topographies (or the correspondence between UR and CR topographies) to include not only US quality (food vs. water) but also variations in fixed-quality food reinforcers. These findings thus confirm the previous report that US size, not confounded by US quality, controls conditional gape amplitudes (LaMon & Zeigler, 1984). The data also extend the findings of Balsam et al. (1978) by showing that pellet size, as well as feeder-access time, controls response rates and latencies. Finally, the simultaneous recording of key pecks and gapes demonstrated the effects of US magnitude upon measures of response strength in two different response classes.

Response Rates and Latencies

Our experiment provided two independent assessments of US magnitude effects on response latencies. For both key-peck and gape responses, larger US magnitudes produced shorter latencies (greater conditioning; cf. Balsam et al., 1978). Our findings may be related to those of O'Connell and Rashotte (1982), who found that US magnitude controlled the temporal location (but not necessarily the rate) of pecks during the CS period. Similarly in our study, large-pellet CSs produced responses earlier in the CS period than did small-pellet CSs. Taken together these findings confirm that the temporal location (as opposed to rate) of CRs is sensitive to US magnitude.

The finding that US magnitude controlled both key-peck and gape rates in autoshaping was of interest because such effects have sometimes been reported only with extreme differences in US magnitude. O'Connell and Rashotte (1982), for example, failed to obtain differences in overall peck rates during CSs that signaled 2 versus 10 pellets (Experiment 1). When the difference in magnitude was increased to 1 versus 15 pellets (Experiment 2), response rates were higher during the CS that signaled the greater magnitude. In contrast, Balsam and Payne (1979) found no effect when feeder-access times were very discrepant (4 s vs. 60 s) while CS and ITI duration were constant. Other studies have found response-rate differences to depend on procedural details. Balsam et al. (1978), for example, obtained rate differences when feeder-access time was varied within sessions, but not when it was varied across sessions. Similarly, failure to show a US magnitude effect also occurred with the between-subjects design of Balsam and Payne (1979) and O'Connell and Rashotte (1982; Experiment 1), whereas the rate differences reported by O'Connell and Rashotte (1982; Experiment 2) were obtained when US magnitude was varied within sessions. The within-session

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amplitudes of the first gape in each trial during the CS period, and the bottom graph shows amplitudes of the first gape during the US period before contact with the pellet. The dotted lines at zero indicate no difference between small-pellet and large-pellet trials.

scheduling of different US magnitudes may also have contributed to the present results.

The failure of some studies to demonstrate US magnitude effects on response rates may depend on performance limitations rather than on conditioning variables (cf. Gibbon, Baldock, Locurto, Gold, & Terrace, 1977). For example, Perkins et al. (1975, Experiments 7 and 8) reported that for different groups of pigeons, response rates were lower with small US magnitudes than with large ones. However, low response rates were mainly observed in the group with feeder-access times of 1 s, which, as noted by Balsam and Payne (1979), may have been too short for birds to obtain food reliably. Thus, low response rates in small-magnitude trials may have been caused by diminished probability of contact with the US rather than by small US magnitudes per se. In the present study US magnitude was varied by pellet size, which ensured that the probability of contact with the food per CS was always 1.0. Any performance limitation, therefore, would affect all trials equally.

Manipulating US magnitude by pellet size rather than by feeder-access time is preferable because it keeps the temporal parameters of the conditioning situation more nearly constant and does not affect the overall frequencies of US and CS presentation. It also avoids the confounding of magnitude with US duration, US quality, US probability, water or food deprivation, and number of URs per US presentation. However, pellet size (diameter) covaries with weight and caloric value as well as with the topography of the eating response elicited by the pellet (small or large gape). Any of these factors, therefore, may have been the critical US dimension that controlled CR rates and topographies in the present experiment.

Our results may also be relevant to the issue of operant contributions to the control of CR rates in autoshaping. It has been noted that there is always an implicit response–reinforcer relation in autoshaping procedures (cf. Gormezano & Kehoe, 1975). Key-directed pecks are followed closely in time by the delivery of food, which may reinforce these pecks directly. The results of this study are subject to the same interpretation. Operant behavior is well known to be sensitive to the magnitude of reinforcement contingent upon its occurrence (e.g., Navarick & Fantino, 1976). Thus pecks or gapes during the large-pellet CS may be strengthened, in an operant sense, to a larger degree than responses during the small-pellet CS. The observed dependence of response rates on US magnitude may thus reflect the operation of operant rather than classical conditioning.

The introduction of a second response key in the third condition produced results that may be relevant to this question. We originally hoped that the second key would enhance control by the CSs by increasing CS discriminability, but this did not happen. Instead, the major effect was an increase in variability, especially for key-peck rates (Figure 2). For P1 and P3 it appeared initially that small pellets produced higher peck rates than large pellets, whereas for P2 and P4 large pellets appeared to boost peck rates beyond the level of the previous condition despite identical size-color correlations. The absolute response rates (Appendix) indicated that this outcome was primarily due to very low overall key-peck rates on the left key (independent of its association with pellet size), which in turn were almost certainly due to the early training conditions when only the right key was accessible. In contrast, gape rates were little disturbed by the introduction of the second key. Several reasons for the differential effects of this manipulation upon peck rates and gape rates may be suggested. First, differences in the recording properties of the keys (position was not counterbalanced) would have differentially affected key-peck but not gape rates. Second, differential peck rates may have reflected the pigeons' tendency to remain close to the right key because of prior reinforcement (cf. B. Brown, Coleman, & Elefant, 1983), thus decreasing performance on the left key. Differential positioning would affect peck but not gape rates. Third, if it were assumed that gapes were under Pavlovian control, whereas key pecks were under operant control, then the expected pattern would be exactly what was actually observed. The position-specific operant contingencies would affect key pecks, which involve directed movements towards the keys, but would not affect gapes, which could occur anywhere in the chamber. Some studies show, in fact, that pigeons' conditional key pecking is a compound response, dissociable into head transport (neck) and gape (jaw) components (Mallin & Delius, 1983; Remy & Zeigler, 1993). The design of our study does not allow strong conclusions to be drawn, but the findings may suggest a strategy for dissociating response–reinforcer from CS–US contingencies. For example, an operant omission contingency could be scheduled for key pecks (e.g., Williams & Williams, 1969), and the effects on peck and gape rates could then be compared.

Response Topography

The finding that conditional gape topography was controlled by pellet size extends the range of conditions known to produce similar effects. Topographical similarities between key pecks and consummatory responses develop in operant paradigms even when no specific response form is reinforced (LaMon & Zeigler, 1984; Spetch, Wilkie, & Skelton, 1981; Wolin, 1968; Woodruff & Williams, 1976) and in autoshaping studies with response-independent food or water delivery (Jenkins & Moore, 1973; LaMon & Zeigler, 1984, 1988; Woodruff & Williams, 1976) even when movements towards the CS are prevented through head fixation (Remy & Zeigler, 1993).

An unusual feature of our data is that both stimulus and response parameters (pellet size, conditional and unconditional gapes) share a common metric (see also LaMon & Zeigler, 1984). This permits quantitative comparisons of the relations among these variables. One such comparison indicates that both conditional and unconditional gape amplitudes were substantially larger than actual pellet sizes. For URs, such overshooting may reflect the functional requirements of the prehensile pecking response (cf. Balsam, Deich, & Hirose, 1992, Figure 7; Bermejo, Allan, Houben, Deich, & Zeigler, 1989, Figure 1; LaMon & Zeigler, 1984, Figures 1 and 2; Zeigler, Levitt, & Levine, 1980, Figure 3). Such considerations do not readily account for the comparable overshooting of conditional gape amplitudes, whose determinants remain to be identified. Similarly, a comparison between the amplitudes of conditional gape responses signaled by small-pellet and large-pellet CSs indicated that this difference was considerably smaller than the actual difference between the two pellet diameters (9.2 mm − 4.9 mm = 4.3 mm). This finding may reflect the effects of pretraining when one white keylight was paired with both pellet sizes and produced CR gapes with intermediate amplitudes independent of CS color or position. (Stokes & Balsam, 1991, for example, have shown that response patterns acquired initially can persist throughout extensive training.) Alternatively, small gape differences may represent response generalization that was engendered by the continuous switching between smaller and larger gapes as US size changed from trial to trial. Many gapes of intermediate amplitude occurred during CSs that signaled either small- or large-pellet size. Response forms intermediate with respect to topography (i.e., displaying topographic features characteristic of both eating and drinking responses) have also been observed in autoshaping studies involving food and water USs (Jenkins & Moore, 1973; LaMon & Zeigler, 1988). Such intermediate response forms may therefore reflect a general effect of discrimination procedures.

The observation that the difference in unconditional gape amplitudes increased over the first, second, and fourth conditions is not easily reconciled with the prevailing assumption that gape amplitudes during the US period are unconditionally and exclusively controlled by properties of the US. That assumption predicts that differences in UR gapes should have remained constant throughout at 4.3 mm (the difference between the actual pellet sizes). Our finding is reminiscent of a phenomenon that has come to be known as the UR diminution effect (Kimmel, 1966). A number of studies, usually involving human subjects and aversive USs, have found that signaled (and therefore predictable) USs produce different (usually smaller) URs than do unsignaled (unexpected) USs (cf. Kamin, 1968, 1969). Our findings may represent the appetitive case of this phenomenon. Perhaps appetitive URs become greater in magnitude (UR potentiation) as conditioning of a CS progresses, that is, as the US becomes increasingly expected over training. (In our study, increases in UR gape differences were indeed due to increases in large-pellet gape amplitudes and not to decreases in small-pellet gape amplitudes.) Note that B. Brown et al. (1983) reported that UR potentiation did not, in fact, occur with pigeons and autoshaping. But they assessed changes in the UR in terms of latency to approach food, which, in contrast to the gape measure in our study, is not an obvious measure of topography.

The present study demonstrated that US magnitude controls both conditional response strength and topography in autoshaping. Moreover, by avoiding most of the confounding effects associated with previous studies of magnitude, it narrowed the range of US dimensions that mediate effects of magnitude. The study also introduced a procedure for the simultaneous recording of response strength and topography in the same subject. This provides a technique to measure these two dimensions of a single response class in future studies that involve manipulations of US properties.

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APPENDIX

The mean number of peck and gape responses, peck and gape latencies, gape amplitudes (for conditional and unconditional responses), and beak resting positions for all birds, for small- and large-pellet trials, for four conditions, and for selected sessions.

Condition and session	P1		P2		P3		P4	
	Small	Large	Small	Large	Small	Large	Small	Large
Number of pecks per 6-s CS								
One-key baseline								
1[a]	1.06	3.50	1.17	4.44	4.33	5.11	0	0.39
5	5.94	13.28	13.89	19.00	7.89	9.61	1.39	2.78
10[b]	6.50	17.89	14.06	20.78	9.78	10.78	0	2.89
15[c]	5.00	20.00	16.28	24.89	8.61	13.06	0.22	4.44
One-key reversal								
1	18.83	3.06	22.58	13.91	4.33	3.56	2.72	0.00
5[d]	6.22	6.56	19.72	22.61	7.61	8.33	0.11	0.06
10	5.94	10.11	11.94	25.06	11.06	14.33	0.17	1.11
Two-key baseline								
1	9.22	4.11	1.39	22.33	11.11	6.56	0.11	1.17
5	8.06	8.28	3.50	18.83	7.17	4.78	0	0.50
10	3.00	6.67	7.06	22.28	1.11	2.00	0	0.61
15	3.28	6.83	8.39	22.50	2.61	0.44	0	1.33
Two-key reversal								
1	6.89	5.22	17.78	5.11	1.28	4.17	0.39	0.00
5	1.06	6.61	14.22	16.11	3.28	11.33	0.06	0.06
10	0.28	9.61	16.33	22.67	0.22	7.61	0.06	0.33
Number of gape responses per 6-s CS								
One-key baseline								
1[a]	2.17	6.67	4.78	10.61	8.78	12.11	0	0.78
5	8.44	15.50	19.11	26.83	21.72	28.22	1.94	4.61
10[b]	8.33	20.33	16.83	27.50	21.33	26.17	0.28	3.67
15[c]	6.22	20.89	20.06	29.28	24.94	34.33	0.72	7.11
One-key reversal								
1	20.50	4.94	27.83	17.00	14.67	13.56	4.33	0.06
5[d]	9.83	9.78	27.44	32.28	18.78	18.78	2.39	0.94
10	10.61	16.61	15.50	31.67	27.33	31.67	2.33	6.22
Two-key baseline								
1	13.17	9.44	3.11	28.44	21.89	26.50	0.94	3.44
5	10.83	12.67	8.61	30.94	18.61	30.17	0.06	4.33
10	5.28	15.44	13.89	30.56	9.94	19.06	0.44	5.78
15	6.44	12.06	13.11	31.61	14.39	18.39	0	5.39

APPENDIX

(*Continued*)

Condition and session	P1		P2		P3		P4	
	Small	Large	Small	Large	Small	Large	Small	Large
Two-key reversal								
1	13.94	10.78	24.22	10.22	19.83	13.72	6.11	0.83
5	7.06	14.06	19.22	21.44	17.28	18.33	1.61	1.83
10	5.11	16.44	22.89	29.33	12.67	9.50	0.28	2.94
Latency (in seconds) of first peck to CS								
One-key baseline								
1[a]	2.99	1.95	2.72	1.76	1.31	2.04	—	1.21
5	0.96	1.13	1.93	1.01	1.35	1.51	1.67	0.96
10[b]	2.22	0.81	2.16	1.26	1.85	1.27	—	1.53
15[c]	2.59	0.84	1.91	0.99	2.78	1.05	3.36	1.80
One-key reversal								
1	0.86	3.02	0.93	2.41	1.49	3.19	1.99	—
5[d]	1.63	1.19	1.59	1.17	1.28	1.59	4.56	2.69
10	2.68	1.51	3.02	0.90	1.46	1.21	5.02	2.57
Two-key baseline								
1	1.96	3.61	3.99	1.38	1.46	1.37	3.63	2.79
5	3.17	2.02	4.10	1.30	2.08	1.58	—	3.34
10	4.23	2.39	3.29	1.23	3.84	3.03	—	2.52
15	4.64	3.68	3.53	1.07	3.50	4.32	—	2.88
Two-key reversal								
1	3.73	4.15	1.77	3.42	2.60	3.12	4.06	—
5	4.94	2.93	1.96	2.11	2.29	1.24	3.12	5.95
10	5.37	1.96	2.24	1.69	4.86	1.60	3.20	3.85
Latency (in seconds) of first gape to CS								
One-key baseline								
1[a]	1.82	1.29	1.46	1.22	1.20	1.38	—	1.52
5	0.86	1.07	1.32	0.93	0.72	0.69	1.53	0.79
10[b]	1.63	0.67	2.02	1.16	0.72	0.85	3.70	0.99
15[c]	2.03	0.79	1.55	0.83	0.74	0.66	2.22	0.83
One-key reversal								
1	0.79	1.78	0.88	2.05	0.64	1.07	1.38	3.43
5[d]	1.17	0.83	1.27	1.11	0.76	0.99	2.46	2.35
10	1.95	0.95	2.39	0.83	1.02	0.84	2.04	1.64
Two-key baseline								
1	1.12	1.33	3.26	1.11	1.12	0.67	2.90	2.48
5	2.41	1.11	3.17	1.08	1.50	0.83	5.15	2.73
10	3.51	1.65	1.79	1.00	1.45	0.97	3.85	1.57
15	3.75	2.57	2.58	1.00	1.78	1.34	—	1.90
Two-key reversal								
1	2.63	2.78	1.24	2.37	0.87	1.75	1.85	3.28
5	2.95	1.03	1.71	1.28	1.47	1.07	2.82	2.96
10	2.89	1.37	1.72	1.22	0.59	0.49	3.91	2.90
Amplitude (in millimeters) of first gape during CS								
One-key baseline								
1[a]	9.26	11.39	11.42	11.24	12.01	12.24	—	9.03
5	11.19	14.22	9.49	11.51	14.77	13.97	10.82	10.72
10[b]	11.26	14.42	8.37	11.46	12.99	13.05	4.50	12.39
15[c]	10.32	14.69	10.62	11.27	9.67	13.67	12.05	11.73
One-key reversal								
1	13.15	9.17	10.45	9.12	15.29	10.97	10.80	9.40
5[d]	14.02	12.68	9.03	11.18	16.71	16.82	6.63	5.37
10	12.41	13.29	8.26	11.05	15.14	13.68	8.73	11.78

APPENDIX

(*Continued*)

Condition and session	P1		P2		P3		P4	
	Small	Large	Small	Large	Small	Large	Small	Large
Two-key baseline								
1	10.67	11.87	8.93	9.93	15.53	11.74	6.49	11.35
5	11.44	11.22	7.28	10.37	13.90	16.23	4.50	13.76
10	13.49	12.56	7.10	9.58	10.94	14.50	13.87	10.82
15	13.85	13.63	7.97	12.57	13.07	17.29	—	12.21
Two-key reversal								
1	13.58	11.92	11.39	9.73	13.53	14.22	11.66	9.23
5	13.41	10.68	11.55	12.11	15.90	16.48	9.92	8.93
10	9.92	13.09	9.05	9.89	9.35	10.58	8.98	9.40
Amplitude (in millimeters) of first gape during US								
One-key baseline								
1[a]	6.31	9.66	8.88	11.53	7.38	10.75	6.74	10.01
5	5.92	8.93	7.43	11.03	8.75	13.19	7.79	11.47
10[b]	7.37	10.67	6.63	11.17	7.62	12.51	7.32	13.83
15[c]	6.47	10.93	6.94	11.32	8.27	12.59	7.29	12.70
One-key reversal								
1	7.15	9.59	7.12	10.53	9.91	13.05	7.48	10.24
5[d]	6.86	9.68	7.14	11.15	9.74	14.58	8.14	11.98
10	6.33	9.41	6.70	11.07	9.49	15.02	8.51	13.81
Two-key baseline								
1	6.73	9.15	6.45	9.87	9.46	12.49	6.48	12.98
5	6.83	9.59	6.08	11.28	9.09	13.49	8.56	15.54
10	8.02	11.67	7.10	11.88	9.88	15.68	8.64	15.55
15	8.24	11.34	6.67	12.18	8.78	13.68	8.24	14.02
Two-key reversal								
1	8.55	10.77	7.16	10.41	9.38	13.63	9.51	14.72
5	8.92	12.38	7.72	12.66	10.04	15.15	8.82	15.24
10	8.83	12.01	8.09	12.93	11.14	16.19	9.29	16.23
Resting position (in millimeters) during CS: Modal value of gape amplitude								
One-key baseline								
1[a]	−2.27	−1.73	−1.13	−0.99	0.19	0.39	−0.42	−0.41
5	−0.74	−0.38	−0.50	0.26	−0.14	0.33	−0.65	−0.55
10[b]	−0.28	0.90	−0.23	0.52	0.46	1.01	−1.57	−1.34
15[c]	−0.96	0.16	−0.29	0.68	0.45	1.11	−1.14	−0.72
One-key reversal								
1	0.74	−0.08	−0.02	−0.95	2.32	1.61	−0.11	−0.35
5[d]	−0.01	−0.13	−0.06	0.40	1.01	1.28	−0.39	−0.45
10	0.39	0.93	−0.77	1.19	1.92	2.07	−0.09	0.04
Two-key baseline								
1	1.15	1.22	−1.59	0.39	1.77	1.76	0.34	0.52
5	0.17	0.45	−0.96	1.09	0.89	1.28	−0.74	−0.27
10	−0.23	0.96	−0.27	1.92	1.04	1.82	−0.77	−0.40
15	0.46	0.99	−2.01	0.38	1.33	1.91	−0.76	−0.34
Two-key reversal								
1	1.31	0.88	−0.28	−1.52	1.76	1.47	0.53	0.24
5	0.88	1.48	−0.02	0.41	2.55	2.89	0.23	0.28
10	0.05	1.07	0.96	2.03	2.86	4.01	−0.15	0.04

[a] Session 2 for P3 and P4, because no responess occurred during the first session.

[b] Session 9 for P1 and P2, because data recording in Session 10 failed.

[c] Session 14 for P2, because data recording in Session 15 failed.

[d] Session 4 for P4, because data recording in Session 5 failed.