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ORIGINAL ARTICLE

Cooperation and Metacontingency in Pigeons

Saulo Missiaggia Velasco[1] · **Marcelo Frota Lobato Benvenuti**[2,3] ·
Angelo A. S. Sampaio[2,4] · **Gerson Yukio Tomanari**[2,3]

Abstract Three pairs of pigeons were exposed to a procedure that combined features of classic studies on social behavior (cooperation) and recent studies that were inspired by the notion of metacontingency. We examined interactions between simultaneous demands for behavior of individual pigeons and interlocked behaviors of pairs of pigeons. The pigeons worked face to face in an operant conditioning box that was divided by a transparent wall. Each side of the box had two horizontally aligned response keys on the floor. Working individually, each pigeon produced 3-s access to food (individual consequence). In a subsequent phase, if the pigeons coordinated their responses, then they could produce food for an additional 4 s (mutual consequence). Initially, the individual consequence was produced on more than 75% of the trials. The interlocking pattern that was required to produce mutual consequences in the subsequent phase was observed on less than 50% of the trials for all pairs of pigeons. Adding the mutual contingency of reinforcement led to (a) a slight reduction of the production of individual and mutual consequences without any coordinated response pattern; (b) the maintenance of high percentages of individual consequences with a concomitant increase in mutual consequences; and (c) for only one subject, an increase in the production of mutual consequences that were accompanied by a decrease in the rate of individual consequences. We discuss the ways in which cooperation and metacontingency experiments should be integrated, the ways in which interlocking behaviors of nonhuman animals can be generated, and the role of verbal behavior in the emergence of cooperation and cultural processes.

Keywords Social behavior · Cooperation · Mutual reinforcement · Cultural selection · Metacontingency · Pigeons

Social behavior, social learning, and cultural evolution are topics that intersect several academic disciplines, including biology, psychology, anthropology, and sociology (Boyd & Richerson, 2005; Heyes & Galef, 1996; Mesoudi, 2011; Tomasello, 2016). Skinner (1953, 1981) sought to integrate contributions from biological, behavioral, and social sciences by proposing a causal mode of selection by consequences as a way to explain the role of the environment in guiding the evolution of a species, behavior, and culture. The relationship between behavior and cultural evolution, however, is a topic that still demands further empirical and theoretical work in both the behavioral and cultural evolution sciences (Boyd & Richerson, 2005; Mesoudi, 2011).

Conceptual and methodological inconsistencies in the study of cultural evolution may arise, for example, from defining cultural units as abstractions (Baum, 2000) and from the lack of a clear conceptual framework to understand what happens when groups of individuals coordinate behaviors and

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✉ Saulo Missiaggia Velasco
saulomv@usp.br

[1] Centro Paradigma de Ciências e Tecnologia do Comportamento, Rua Wanderley, 611, São Paulo 05011-001, Brazil

[2] Instituto de Psicologia, Universidade de São Paulo, São Paulo, Brazil

[3] Instituto Nacional de Ciência e Tecnologia sobre Comportamento, Cognição e Ensino, São Carlos, Brazil

[4] Colegiado de Psicologia, Universidade Federal do Vale do São Francisco, Petrolina, Brazil

generate products that are contingent on this coordination (Smaldino, 2014). Based on Skinner's work, Glenn (1986, 1991, 2003, 2004) specifically addressed interactions between behavior and cultural selection, stressing the role of units that comprise the interlocked behaviors of two or more individuals and their products in a contingency of cultural selection she called *metacontingency.* Despite Glenn's conceptual contributions, a clear empirical framework that demonstrates the ways in which behavior interacts with cultural processes is still needed. In the present study, we addressed this issue by programming mutual consequences for the interlocked behaviors of two pigeons working for a common gain. At the same time, consequences for the individual behaviors of each pigeon were also available.

Classic experiments on cooperation (e.g., Azrin & Lindsley, 1956; Cohen & Lindsley, 1964; Mithaug & Burgess, 1968; Schmitt & Marwell, 1968; Skinner, 1962) have been conducted with both human and nonhuman subjects. In these experiments, the coordinated responses of two or more individuals were correlated with specific consequences (for a methodological review, see Schmitt, 1998). Skinner, for example, demonstrated cooperation in two pigeons that worked in adjacent compartments of the same experimental chamber separated by a transparent wall. Three response keys were arranged vertically on each side of the wall, such that each key on one side was horizontally aligned with a corresponding key at the same height on the other side. At each moment, only one pair of adjacent same-height keys was randomly designated as effective for food production if both pigeons pecked the respective keys within a time interval of ≤0.5 s. Thus, to produce food, the pigeons had to cooperate in two tasks: (a) explore the three pairs of keys until the effective pair was found and (b) simultaneously peck both keys of that pair. Skinner (1962) demonstrated that "these contingencies sufficed to build cooperative behavior without further attention" (p. 533) and that a division of labor developed in the task. One pigeon (i.e., the leader) explored the keys, pecking each one randomly. The other pigeon (i.e., the follower) pecked the key that was opposite to the one that was pecked by the leader.

Using an experimental protocol that was quite similar to the one used by Skinner (1962), Tan and Hackenberg (2016) established additional experimental controls to elucidate the effects of "mutual reinforcement" on "mutual responses" in rats. The authors defined *mutualism* as a type of cooperation "in which socially coordinated behavior produces gains for both animals" (p. 13). They conducted three experiments. In the first experiment, the effects of the mutual reinforcement contingency were compared with the effects of reinforcement that was provided at the same rate but in yoked-control conditions, thus without the temporal requirement for coordination. In the second experiment, coordinated behavior was compared across different types of barriers that separated the rats (i.e., transparent, opaque, and wire mesh), with an additional condition that consisted of no barrier at all. In the third experiment, coordinated behavior was compared when the rats worked with familiar and unfamiliar partners. The results indicated the following: (a) Only contingencies of mutual reinforcement systematically produced coordinated behavior by pairs of rats, (b) the types of barriers and their presence or absence did not affect coordinated behaviors, and (c) coordinated behavior was maintained even after a familiar partner was switched to an unfamiliar partner. These data increase the generalizability of Skinner's (1962) results, stressing the importance of basic research with nonhumans to investigate different aspects of cooperative behavior.

Marwell and Schmitt (1975) investigated cooperation in human participants using a setting in which pairs of undergraduate students produced points that could be exchanged for money when a response from one of the students occurred 3–3.5 s after a response from the other student. Schmitt and Marwell (1968) demonstrated that this pattern of temporal spacing was established only when each response by the first participant produced an antecedent stimulus (a 3-s light signal) for the second participant. When the light signal was disabled, cooperative responses occurred at a low rate. Marwell and Schmitt were ultimately interested in the conditions that either promoted or hindered cooperation, and because of that the participants could also work individually for points. Each participant could choose to work individually or cooperatively by operating a toggle switch with the labels *work alone* and *work with other person*. A cooperative response could be performed only if both participants chose to work together. If either or both chose to work alone, each response by one participant was independently reinforced with points. Therefore, unlike Skinner's (1962) procedure, Marwell and Schmitt's procedure used a concurrent schedule in which the participants had to choose between the individual and cooperative contingencies.

The concept of metacontingency was recently introduced within the context of experimental research to investigate the effects of consequences that are contingent on the aggregated products of people's behavior as part of a group. Vichi, Andery, and Glenn (2009) programmed consequences that were contingent on aggregate outcomes of a consensual group decision. In successive trials, quartets of undergraduates individually bet tokens that were exchangeable for money. They then consensually made a common choice. On each trial, the group could double or lose half of the tokens that were bet. Afterward, the quartet consensually decided how to divide the resulting tokens among the participants. The success or failure of the bet (i.e., the programmed consequence) depended only on whether the tokens were divided equally or unequally in the previous trial (i.e., the aggregate outcome of interest). The relevant interaction that was measured was the consensual decision about the division of gains at the end of each trial.

The quartets systematically produced equal or unequal divisions of tokens when one or the other aggregate outcomes resulted in doubled tokens (i.e., the programmed consequence). Based on Glenn's work (1986, 2004), Vichi et al. (2009) referred to the observed dependency between participants' coordination (or interlocked behaviors) and programmed consequence as a metacontingency. Increases in the rate of interlocking behaviors implied increases in both the behavior of each participant and the social consequences and/or social antecedents that in fact are changes in the other participants' behavior. Because of these characteristics, metacontingency may be viewed as a unit of analysis at Skinner's (1981) cultural level of selection by consequences.

In the study conducted by Vichi et al. (2009), similar to other studies on cooperation (e.g., Azrin & Lindsley, 1956; Skinner, 1962), the only way to gain tokens was to coordinate responses with other participants. In contrast, other experiments have superimposed the mutual contingency on individual contingencies to allow concomitant study of the ways in which behavior and group organization may be affected by different consequences or magnitudes of the same consequence (e.g., Pavanelli, Leite, & Tourinho, 2014; Saconatto & Andery, 2013; Sampaio et al., 2013; Toledo et al., 2015). In such studies, individual contingencies were compatible with the mutual contingency such that participants' responses could simultaneously produce consequences that correlated with what they did individually and mutually.

An important starting point for building integrative experiments in the field of basic cultural processes is to review the cooperation study by Skinner (1962) from the perspective of metacontingency (for a detailed analysis, see Hunter, 2012). One argument is that activation of the feeder in Skinner's study was correlated with interlocking behavior (i.e., responding under control of the behavior of the other subject) and its aggregated product (i.e., simultaneously pecking the same-height key pair). However, as in the study by Vichi et al. (2009), the only way to produce activation of the feeder was by coordinating the actions of both subjects. Although an individual contingency in cooperation studies is generally arranged as a concurrent alternative to cooperation (e.g., Marwell & Schmitt, 1975), demands for coordination in metacontingency studies (e.g., Pavanelli et al., 2014; Saconatto & Andery, 2013) are usually compatible with demands for what the participants do individually (i.e., participants' responses can produce individual and mutual consequences simultaneously). The present study sought to integrate these different lines of investigation by adding to Skinner's (1962) procedure an individual contingency of reinforcement upon which the mutual contingency was superimposed. We propose that such a manipulation will help distinguish units that may be defined by individual behavior from others that can be defined by interlocked behaviors. Such conditions allow us to examine interactions and possible conflicts between what is demanded by each pigeon individually and mutually as a member of a group.

As a possible animal model of metacontingency (also see Gimenes, 2016), the present study sought to answer another question: Is behavior related to the notion of metacontingency characteristically human? Human cultures certainly have unique aspects, and verbal behavior is responsible for many of those. To study the uniqueness of human cultures, an animal model of metacontingency may not necessarily be useful. However, metacontingency is a relatively new conceptual tool that "makes it possible to treat group behavior in terms of behavioral contingencies, without the traditional conflict between individual and society" (Todorov, 2010, p. 87). As a new tool, the concept is being delineated by continuous efforts in the fields of conceptual, applied, and basic research (for a broad review of applied possibilities to generate prosocial behaviors and cultural changes, see Houmanfar, Alavosius, Morford, Herbst, & Reimer, 2015, and Malott, 2016).

As a recent proposition, the concept of metacontingency has been criticized, and some authors have questioned whether the concept is really necessary (e.g., Carrara & Zilio, 2015; Krispin, 2016). A review of the literature that uses the term *metacontingency* also highlights at least three critically different uses of terminology. Todorov (2012) stated that metacontingency may mean (a) nonrecurring long-term phenomena, such as social movements; (b) descriptions of correlations between behavior and outcomes, such as in laws; and (c) units of analysis to study interactions between interlocking behavioral contingencies—their aggregate products and consequences dependent on such products—in laboratory experiments. Therefore, the fundamental characteristics of a metacontingency, its proper use, and its characterization are still being debated. Basic investigations with nonhuman subjects may critically contribute to this debate. As Catania (2013) noted, "we have to be able to identify events before we can study their properties. One place to start is to look at behavior that does not involve language" (p. 4). The present study sought to identify the behaviors and environmental events that may characterize a metacontingency as a distinct tool in the science of behavior.

Method

Subjects

Six naive adult pigeons (*Columba livia*) were used. Each pigeon was individually housed in a 50 × 50 × 50 cm living cage. Lights in the colony room were programmed with a light–dark cycle of 13 and 11 h, respectively, with lights on at 8:00 a.m. Each animal was maintained at 80% of its ad libitum weight by food restriction and was fed only during the experimental sessions. Water, grit (an oyster meal and charcoal compound), and bird toys were freely available in the living cages. A vitamin supplement was added to the subjects' water three times per week.

Equipment

A custom-built operant conditioning chamber was equipped with MED Associates components (Fig. 1). A transparent wall or opaque barrier divided the chamber into two 40 × 35 × 45 cm compartments, controlling whether a pigeon in one compartment could see the pigeon in the other compartment. In each compartment, two translucent response keys (3 cm in diameter) were located 4 cm above the floor, facing up. The keys were horizontally aligned at a distance of 1 cm from the transparent wall. The keys could be illuminated with a green, red, or white backlight. The two pigeons had to stand in front of each other to peck the keys.[1]

Each compartment also contained a third response key on the wall opposite the transparent wall. This key was illuminated only by a white light. The wall opposite the transparent wall also contained the food tray, which was centered on the wall 8 cm above the floor. When triggered, each feeder was illuminated by a 7.5-W incandescent light and allowed access to a grain mixture. Another 7.5-W incandescent house light, located 20 cm above the food tray, illuminated each compartment. In each compartment, an exhaust fan was mounted on the wall opposite to the transparent wall, providing air circulation and reducing external noise. A closed-circuit television system filmed and recorded the experimental sessions. The chamber was connected to a computer that controlled and recorded the experimental events through software that was developed for this study.

Procedure

Preliminary Training

Initially, 60-trial sessions of autoshaping were conducted with only one subject at a time in the chamber and with the opaque barrier dividing the experimental box. At the beginning of each trial, the key above the food tray was illuminated. After 8 s, the key light was turned off, and access to food was allowed for 4 s. If the subject pecked the key before 8 s elapsed, then the key was turned off, and food was presented for 4 s, followed by a 60-s intertrial interval (ITI). We conducted daily autoshaping sessions with each subject until key-pecking stabilized. The subjects were then exposed to a 10-s fixed interval with a 2-s limited hold (FI10 LH2) schedule of reinforcement and an 18-s ITI. We conducted daily sessions under an FI10 LH2 schedule with each subject until the moving average of reinforced trials in the last 10 sessions reached at least 79%.

Experimental Phases

The preliminary training was followed by four experimental phases during which the subjects worked in pairs, each in a separate chamber compartment, separated by the transparent wall. When both pigeons were responding on the keys, each pigeon could clearly see the other's behavior. In all four phases, the sessions consisted of sixty 12-s trials with an 18-s ITI. At the beginning of each trial, the four keys (two per compartment) were simultaneously lit with the same color (green or red). The colors were semirandomly presented, with 30 presentations of green and 30 presentations of red per session.

Individual Contingency Phase In the first experimental phase, the subjects were allocated to pairs (S1–S2, S3–S4, and S5–S6), but only an individual contingency (independent of the other's behavior) was programmed in each compartment. At the beginning of each trial, both keys in both compartments were simultaneously illuminated by green or red lights (although the colors were irrelevant in this phase). The first key-peck that was emitted turned off and deactivated the *other* key until the next trial. This procedure was introduced to prevent alternations between the keys within the same trial. Further pecks that were emitted until 10 s after the start of the trial produced no scheduled consequences. A peck that was emitted on an active key between 10 and 12 s after the start of the trial produced 3-s access to food on an FI10 LH2 schedule. If no peck was emitted during the trial, then the key lights were turned off and the ITI started. There were no programmed consequences for pecking the darkened key.

To ensure alternations between the keys across trials, if the pigeon produced reinforcement on the same key in three consecutive trials, then this key became deactivated (producing no further consequences) but remained lit. As in the previous trials, the first peck on the other key turned off the first one. A peck on the key that remained lit between 10 and 12 s after the start of the trial was reinforced. The phase ended when performance stabilized in the presence of both colors and when the responses were approximately equally distributed between the keys. In short, the individual contingency sought to produce the emission of all key-pecks on a trial on the same key and alternation between keys after at least three trials.

Individual and Mutual Contingency Phase In the second experimental phase, a mutual contingency was superimposed on the individual contingency. The individual contingency that was established in the preceding phase was maintained,

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[1] Initially, the response keys were arranged vertically, parallel to the transparent wall that divided the experimental chamber, using an arrangement similar to that of Skinner (1962). However, the pigeons exhibited marked key and position preferences. These preferences were prevented by arranging the keys on the chamber floor.

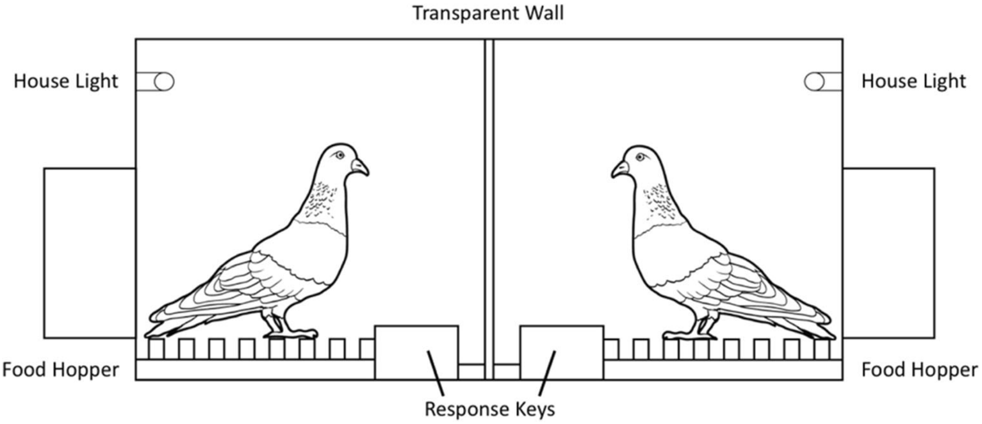

Fig. 1 The custom-built operant conditioning chamber used in the experiment

but if the pigeons responded coordinately, then 4 s of food was also provided. The pigeons could produce one of the following outcomes on each trial: (a) no consequence, (b) only the individual consequence (3-s access to food), (c) only the mutual consequence (4-s access to food), or (d) both consequences (7-s access to food; Fig. 2a). When the keys were lit red, if both subjects responded on parallel keys at an interval of ≤0.5 s between each peck, then 4-s food access was produced (i.e., the mutual consequence). If the subjects pecked diagonally aligned keys (on opposite sides of the partition wall) or if more than 0.5 s elapsed between pecks, then this consequence was not presented. When the keys were lit green, if the subjects pecked diagonally aligned keys at an interval of ≤0.5 s, then 4-s food access was produced. Responses on parallel keys did not produce this consequence (Fig. 2b). The house light flashed at 0.1-s intervals during activation of the feeder by coordinated responses.

Position Interchange Phase After 70 sessions, to test for spurious control by the location of the pigeons in the chamber, the positions of one pair of subjects in the experimental chamber were alternated every 10 sessions. The phase was terminated after six alternations (60 sessions).

Interchange Among Pairs Phase To test whether the behavioral repertoire that was acquired in previous phases would generalize in the presence of other subjects and whether the contingencies that were arranged by a subject would maintain the responding of another subject, we maintained the same contingencies of the previous phase, but the subjects were rearranged into new pairs. Initially, the new pairs were S5–S3 and S6–S4, and then the sessions were performed with the S5–S4 and S6–S3 pairs.

Results

Figure 3 shows the results for all pairs of subjects in all phases of the study. Figure 3a depicts the percentage of individual consequences that were presented in the last 10-session block of the individual contingency phase and the percentage of mutual consequences that would have been presented had they been programmed. Each pigeon produced individual consequences on more than 75% of the trials. On the same 10-session block, pairs of pigeons would have produced mutual consequences on 25%–50% of the trials. Figure 3a also shows the percentage of individual and mutual consequences that were actually produced in the individual and mutual contingency and position interchange phases.

The mutual contingency did not strengthen the coordination of S1 and S2 responses and impaired the production of individual consequences by both subjects. Comparisons of the

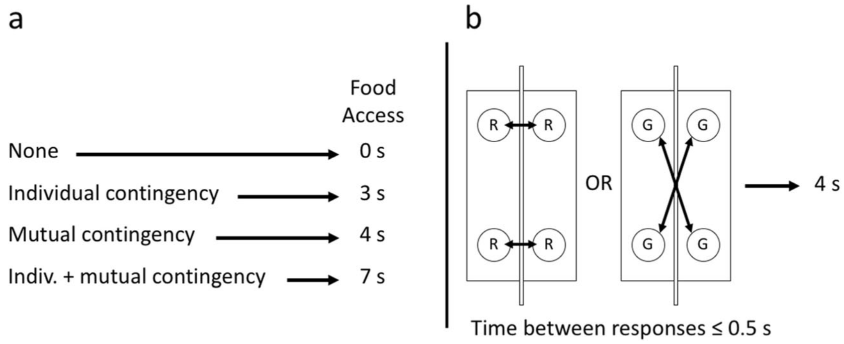

Fig. 2 Summary of experimental contingencies arranged in the individual and mutual contingency phase: **a** duration of food access that was produced by meeting the different contingency requirements and **b** the necessary coordination for the production of mutual consequences (4-s food access for each pigeon). R = red; G = green

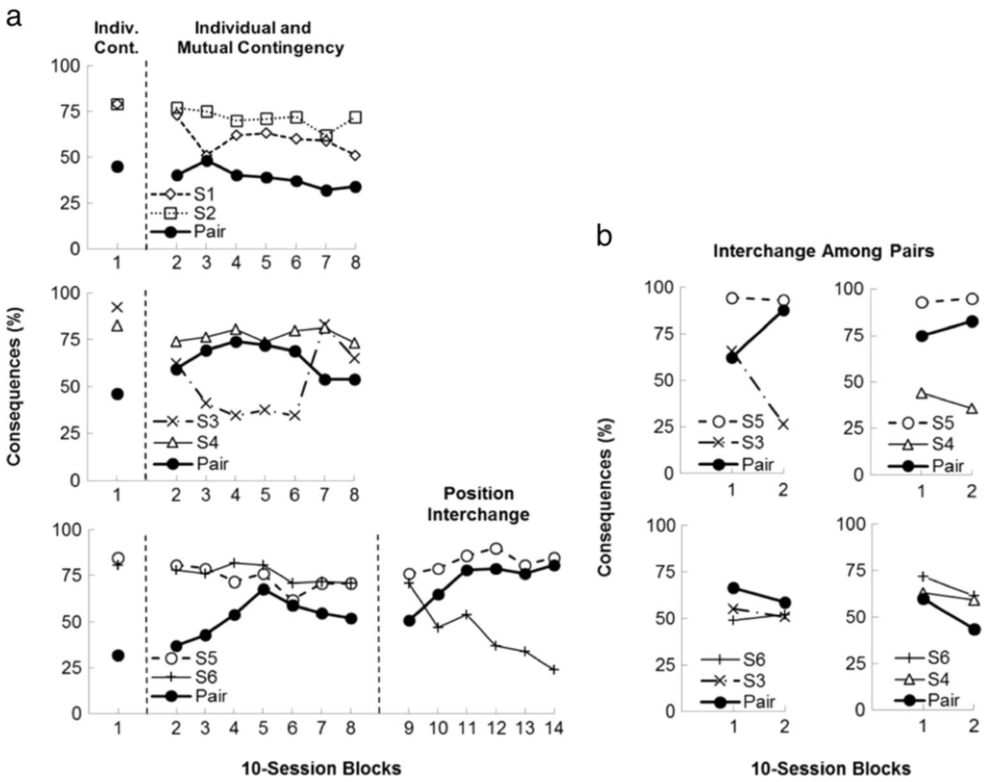

Fig. 3 Percentage of individual and mutual consequences in 10-session blocks for all pairs of subjects. **a** Block 1 is the last block in the individual contingency phase. In that phase, consequences refer to the mutual consequences that would have been presented had they been programmed. **b** The results of the interchange among pairs phase

last blocks of the individual contingency and individual and mutual contingency phases show that the percentage of individual consequences decreased for both S1 (from 79% to 51%) and S2 (from 79% to 72%). The same happened for mutual consequences, which decreased from 45% to 34%. The introduction of the mutual contingency impaired the production of individual consequences for S3 during the first five blocks. During this period, S3 responded on the same key, regardless of its color. S4 pecked the key in front of the one that was pecked by S3 in the presence of the red light and pecked the key diagonally across from the one that was pecked by S3 in the presence of the green light. This pattern did not require social antecedent control by any of the subjects and produced uneven consequences for them (only 4 s of food for S3 but 7 s of food for S4). These consequences, however, were socially mediated: The length of time of feeder access depended on what the other subject did. Finally, in the last two blocks, responses were under control of the individual contingency alone, in which the percentage of mutual consequences for the S3–S4 pair declined, approaching the value that would have been produced in the last block of the individual contingency phase.

The percentage of mutual consequences that were produced by the S5–S6 pair increased until the fourth 10-session block of the individual and mutual contingency phase, without significant reductions of the percentages of individual consequences. This indicates the strengthening of coordinated responses and social antecedent control that is needed to produce mutual consequences with such a frequency. Up to this point, the percentages of individual consequences and food access lengths of time for the two subjects had been similar. From the fifth block onward, however, the frequency of mutual consequences decreased by the end of the phase until it was close to the percentage that would have been produced in the last block of the individual contingency phase. Throughout the individual and mutual contingency phase, the percentage of individual consequences slightly decreased (from 81% to 71% for S5 and from 78% to 71% for S6).

Throughout the position interchange phase, the production of individual consequences by S6 decreased, in which it responded more often on only one key. Because S5 continued alternating between keys according to the corresponding colors, it continued producing both individual and mutual consequences (3 s + 4 s = 7 s of food). At the end of this phase, similar to Blocks 3, 4, and 5 for the S3–S4 pair, S6 was producing individual consequences (3 s) quite rarely but frequently gaining access to mutual consequences (4 s).

Figure 3b shows the results of the interchange among pairs phase. The S5–S3 and S5–S4 pairs presented the same response pattern that the S5–S6 pair had shown throughout most of the position interchange phase. S5 alternated between keys under control of the light color, whereas S3 and S4 continued responding on the same key. Although these results involved socially mediated consequences, they may have occurred without social antecedent control. The S6–S3 and S6–S4 pairs, in contrast, ended this phase with nearly 50% of mutual consequences. S5 was a member of all pairs that produced high percentages of mutual consequences in all phases. The stable behavior of S5 with regard to switching between keys according to the key color and according to the other subject's response was essential for the strengthening of at least one pattern of coordination.

Discussion

The present study examined interactions between demands for behavior of each pigeon in a pair and for interlocked behaviors of pairs of pigeons. We sought to distinguish individual behavior that is maintained by reinforcement from interlocked behaviors that correlated with an increase in the magnitude of reinforcement (mutual consequence). Three pairs of pigeons were first exposed to the individual contingency, and then a mutual contingency was added. At the end of the first phase, the individual consequence was produced on more than 75% of the trials for all subjects, and the patterns of interaction that needed to be coordinated in the subsequent phase to earn a larger magnitude of food (i.e., target interlocked behaviors) were observed on less than 50% of the trials for all pairs.

Adding a mutual contingency of reinforcement led to three distinct tendencies. First, for the S1–S2, S6–S3, and S6–S4 pairs and for the S5–S6 pair in Blocks 6–8, only a slight reduction in the production of individual and mutual consequences was observed. Apparently, coordinated response patterns were not strengthened by the contingent presentation of the mutual consequence. Second, there was a tendency toward the maintenance of high percentages of individual consequences with a concomitant increase in mutual consequences in Blocks 2–5 for the S5–S6 pair. Third, a more frequent tendency was an increase in the production of mutual consequences that were accompanied by a decrease in individual consequences for just one subject in the pair, which occurred in Blocks 2–6 for the S3–S4 pair and in Blocks 9–14 for the S5–S6, S5–S3, and S5–S4 pairs. In these cases, one pigeon responded on only one key, and the other pigeon consistently responded under discriminative control of the key color.

The mutual contingency mainly increased the occurrence of coordinated behaviors in which each individual emitted different responses and obtained different magnitudes of reinforcement. When one pigeon responded on only one key and the other pigeon alternated between keys under control of the key color, the behavior of one pigeon did not have to exert stimulus control over the other's behavior. Thus, the contingency that we arranged differed from the contingencies that were arranged in many cooperation studies (e.g., Marwell & Schmitt, 1975). Nonetheless, in the present study, the pigeons' behavior was clearly interlocked by the mutual reinforcement (as in Tan & Hackenberg, 2016), which is an important aspect of both cooperation and metacontingency studies. Because reinforcement for the behavior of each individual was partially established by the behavior of the other individual, it can be assumed that the behavior and (social) environment were jointly selected by the mutual contingency, which is suggested by the notion of metacontingency.

Metacontingency can be defined as the production of a cultural consequence by interlocking behavioral contingencies (Glenn, 2004; Glenn et al., 2016). The concept of metacontingency has been used in organizational settings, with some authors proposing its integration with behavior system analysis (e.g., Malott, 2016; Malott & Glenn, 2006). Notably, however, the proposed minimum definition of the concept (Glenn et al., 2016) does not restrict itself to applied settings and does not include elements that are typically found in organizational metacontingencies, such as a receiving system or some kind of environmental feedback to the organizational leadership. The concept of metacontingency has also been operationalized experimentally by arranging situations in which an individual's response produces antecedent stimuli for the other's response (e.g., Vichi et al., 2009). If diverse interlocking behaviors can be strengthened in the same experimental setting, however, then they may involve different response costs or different reinforcer magnitudes for the individuals involved, such as in the present study. Thus, researchers should clearly describe all the different kinds of interlocking behavioral contingencies that could emerge in a particular experiment, and theorists should specify the interlocking behavioral contingencies that are covered by the concept of metacontingency.

Although the present experimental design was similar to that of Skinner (1962) with respect to cooperation, describing it within the framework of metacontingency allows one to integrate discussions of social behavior and cooperation with discussions of cultural evolution and cultural selection. Analyses of the results of cooperation and social behavior studies from this perspective may reveal new methodological approaches to study cultural evolution and cultural selection and integrate different research fields (also see Heyes, 2012a, 2012b).

The present study represents an important step toward developing such an integrative approach. However, the notable variability of our data indicates that our procedure needs to be strengthened and refined, and future studies should address some methodological issues. For example, the cooperative task that we assigned to our subjects requires conditional discrimination. For each pigeon, the green- and red-lit keys should have functioned as conditional stimuli that controlled the discriminated operants of pecking opposite to or across from the other pigeon, respectively. On any given trial, the green-lit keys should have established the key opposite to the one that was being pecked by the other pigeon as a discriminative stimulus for pecking. The red-lit keys should have established the key across from the one that was being pecked by the other pigeon as a discriminative stimulus for pecking. An important issue to consider is that such accurate conditional discrimination would require simple discriminations among the conditional stimuli (i.e., the green- and red-lit keys) and the discriminative stimuli (i.e., the other pigeon's position while pecking; Saunders & Green, 1999).

Stimulus control analyses of failures of conditional discrimination have identified the importance of training simple discriminations before attempting to train conditional relations (e.g., Saunders & Green, 1999; Saunders & Spradlin, 1989). Unfortunately, our procedure did not guarantee that these prerequisite simple discriminations were properly established before introducing the mutual contingency. Instead, the red or green discrimination was implicitly rendered irrelevant because the pigeons had a history of responding to the lit keys, and the color of the keys did not influence reinforcement delivery. Therefore, when the mutual contingency was introduced, our subjects had to not only acquire red or green discrimination but also overcome that history of irrelevance. Thus, subjects in future studies might explicitly be taught all of the simple discriminations that are needed to coordinate actions to produce contingent mutual consequences.

In our procedure, the distinction between working individually and working as part of a team can be seen as a matter of choice behavior. When the mutual contingency was in effect, on any given trial each pigeon could choose to work for the individual consequence, for the mutual consequence, or for both consequences. Each choice demands specific stimulus control relations that can be viewed on a continuum of complexity: to produce individual consequences, a simple discrimination was needed, and to produce mutual consequences, conditional discriminations were needed. Thus, choosing to work as part of a team demanded more complex stimulus control relations. From what is known about the distribution of behavior predicted by the matching equation (Herrnstein, 1961), such a difference in alternatives should produce a bias in favor of the less complex alternative (i.e., the one requiring less effort), which may explain our observed variability, at least in part. Whether an increased amount of reinforcement associated with the more complex alternative is enough to override a bias for the less effortful alternative is an empirical matter. Future experiments should use parametric variations of reinforcement duration to explore this issue.

Our results demonstrate that coordinated behaviors of nonhuman animals can be selected by contingencies that are arranged for the pair as a whole, similar to the findings of Skinner (1962). In the present study, we used a procedure that was further inspired by metacontingency studies and that was first suggested by Velasco, Benvenuti, and Tomanari (2012), in which interlocking behaviors were necessary for the production of additional mutual consequences. Based on this type of procedure, we suggest that selection by metacontingencies is possible without the requirement of verbal behavior.

Experimental procedures such as the one discussed herein may be critical for basic research on cooperation and metacontingency because they allow control over verbal behavior and control over overlapping contingencies and metacontingencies. Additionally, the use of nonhuman animals can be critical for integrating evolutionary perspectives on social behavior and culture, highlighting the key role of social behavior and culture in biological evolution (Sampaio, Ottoni, & Benvenuti, 2015). Given the size and importance of this field of research, experimental procedures that allow interdisciplinary dialog will be critical to advance knowledge.

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Compliance with Ethical Standards All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All of the animal procedures were in accordance with the ethical standards of the institution at which the study was conducted.

Conflict of Interest On behalf of all authors, the corresponding author states that there are no conflicts of interest.

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