

## Incentive Contrast in Domestic Dogs (*Canis familiaris*)

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Dogs (*Canis familiaris*) trained to receive a preferred food (dry beef liver) from an experimenter learned to maintain a longer gaze on the experimenter than dogs receiving a less preferred food (dog pellets). Dogs downshifted from dry liver to pellets rejected food more frequently than nonshifted controls. Gaze duration also decreased in downshifted dogs below the level of a group always reinforced with pellets. In addition, downshifted dogs tended to move away from the experimenter, adopting a lying down posture. This phenomenon, called successive negative contrast, has been described in analogous experiments with a variety of mammalian species, but has failed to occur in similar experiments with nonmammalian vertebrates. Unlike similar previous observations, the present data were obtained in an environment involving interspecific communication.

*Keywords:* incentive contrast, frustration, interspecific communication, domestic dogs

Surprising incentive omissions, that is, the absence or reduction of an appetitive reinforcer in the presence of signals previously paired with a larger incentive, have aversive effects and elicit emotional responses (Amsel, 1992; Papini & Dudley, 1997). In a classic example (Tinklepaugh, 1928), a monkey saw the experimenter deposit a reward under one of two cups. After a few seconds, a screen was lowered to introduce a retention interval, while the cups were not under the monkey's view. When the interval was over, the screen was lifted and the monkey could choose one of the two alternatives. If correct, the monkey could consume the reward. On some training trials, the monkey saw either a piece of banana (a preferred incentive) or lettuce (a less preferred, but acceptable, incentive) being placed under the choice cup. However, on occasional test trials, the piece of banana was substituted by lettuce during the retention interval, while view of the cups was occluded. Tinklepaugh described the behavior of a monkey on one of such test trials in these terms:

She picks the cup up and examines it thoroughly inside and out. She has on occasions turned toward observers present in the room and shrieked in apparent anger. After several seconds spent searching, she gives a glance toward the other cup, which she has been taught not to look into, and then walks off to a nearby window. The lettuce is left untouched on the floor. (pp. 224–225)

Converging lines of evidence indicate that surprising reward omissions of this type are accompanied by aversive emotional

reactions, at least in mammals (Papini, 2006). For example, after a surprising reward omission, rats learn new escape responses (Daly, 1974), their agonistic behavior is affected (Mustaca, Martínez, & Papini, 2000), male sexual responses are disrupted (Freidin & Mustaca, 2004), plasma levels of glucocorticoids increase (Mitchell & Flaherty, 1998), dominant responses occur with increased vigor (Stout, Boughner, & Papini, 2003), and such vigor is eliminated by adrenalectomy (Thomas & Papini, 2001). Such reactions to surprising reward omissions can also be reduced or eliminated by treatment with only a restricted set of pharmacological agents, including benzodiazepine anxiolytics and opioids (see Flaherty, 1996; Papini, Wood, Daniel, & Norris, 2006). Similar behavioral and physiological changes have been described in other mammalian species, including marsupials, rodents, artiodactyls, and primates (Papini, 2006; Papini & Dudley, 1997). All together, this evidence provides support for the notion that surprising reward omissions induce an aversive emotional response.

A common paradigm to study surprising reward omissions is known as successive negative contrast (SNC). In a typical SNC experiment (Flaherty, 1996), one group of animals is exposed to a downshift in incentive quality or quantity and the behavior of these animals is compared to that of unshifted controls always exposed to the lower incentive. SNC occurs if the behavior of the downshifted animals is significantly disrupted relative to that of the unshifted controls. More interesting, analogous downshift experiments with nonmammalian vertebrates (including teleost fish, anuran amphibians, turtles, and pigeons) yield evidence of magnitude discrimination, but no evidence of SNC. In such experiments, behavior usually changes gradually in response to the downshift without any evidence of contrast (a reversed SNC effect; see Bitterman, 2000; Papini, 2006). For example, goldfish (*Carassius auratus*) downshifted from 40 to 4 worms after swimming in a runway exhibited little if any change in response latencies, despite showing shorter latencies for the large reward than for the small reward (Lowe & Bitterman, 1967). Such comparative discontinuities provide impetus for research with additional species to determine the taxonomic range of the potential divergence. Additional comparative

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data will contribute to determine whether these species differences reflect a phylogenetic pattern or local adaptations.

Some responses of potential social relevance are known to be affected by incentive downshifts, including crying in human babies (Mast, Fagen, Rovee-Collier, & Sullivan, 1980), ultrasonic vocalizations in infant rats (Amsel, Radek, Graham, & Letz, 1977), and odor emissions in rats (Ludvigson, 1999). As mentioned above, direct assessment of the social behavior of rats immediately following a downshift experience also provides relevant evidence (Freidin & Mustaca, 2004; Mustaca, Martíne, & Papini, 2000). However little is known about the effects of incentive downshifts on communicative behavior.

Because of domestication, dogs have heightened interspecific communicative skills compared to other canids (Hare, Brown, Williamson, & Tomasello, 2002; Miklósi et al., 2003). Several studies have shown the relevance of gaze direction as an indicator of the human attentional focus in communicative tasks between dogs and humans (e.g., Bräuer, Call, & Tomasello, 2004; Call, Bräuer, Kaminski, & Tomasello, 2003). Dogs use their own gaze toward people as a communicative signal (e.g., Miklósi et al., 2003). If food is visible but out of reach, dogs react by looking at the person and alternate its gaze from owner to food (Miklósi, Polgárdi, Topál, & Csányi, 2000). This response is more pronounced than that of other domesticated species, such as cats (Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005) and socialized wolves (Miklósi et al., 2003) in an unsolvable task.

Occasionally, dogs use cues from human behavior without explicit training (e.g., Hare & Tomasello, 1999; Soproni, Miklósi, Topál, & Csányi, 2001) and from an early age (Agnetta, Hare, & Tomasello, 2000; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008). This evidence has led some to suggest that the dog's interspecific communicative skills are species typical and independent from learning (e.g., Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare & Tomasello, 2005). However, there is relatively little information on the effects of learning on human–dog communication. Recently, Wynne, Udell, and Lord (in press) reanalyzed Riedel et al.'s (2008) data and found a significant age effect: older puppies performed above younger puppies in tasks that required human cues. Moreover, young puppies improved their behavior across trials. This evidence suggests that instrumental learning is involved in interspecific human–dog communication.

Similarly, Bentosela, Barrera, Jakovcevic, Elgier, and Mustaca (2008) reported that the dog's gaze directed at an unknown person to solicit food exhibits rapid changes during acquisition and extinction trials. No information is available, however, about the effects of a surprising reduction in incentive value on human–dog communication—the aim of the present experiment.

## Method

### Subjects

The subjects were 13 adult dogs (*Canis familiaris*; see Table 1 for details). Dogs were recruited voluntarily from their owners. All the observations reported here were made in Buenos Aires, Argentina, in the period between March and December 2006. At the time of training, dogs were living in their home, where they had free access to water. The last meal before training sessions had been received between 8 and 12 hr earlier for large dogs (more

Table 1  
*Description of the Sample Used in This Study*

Subject No.	Age <sup>a</sup>	Sex	Breed	Group
1	126	Female	Mixed	Downshifted
2	240	Female	German Shepherd	Downshifted
3	168	Female	Mixed	Downshifted
4	48	Male	Samoyed	Downshifted
5	144	Male	Springer Spaniel	Downshifted
6	312	Male	Siberian Husky	Downshifted
7	72	Male	Shih Tzu	Downshifted
8	72	Female	Rottweiler	Unshifted
9	144	Female	Mixed	Unshifted
10	72	Female	Labrador	Unshifted
11	72	Female	Great Dane	Unshifted
12	6	Male	Labrador	Unshifted
13	33	Male	Poodle	Unshifted

<sup>a</sup> Given in months.

than 10 kg in weight), but between 14 and 18 hr for small dogs (less than 10 kg in weight).

### Procedure

All sessions were scheduled in the dog's home. Sessions were scheduled in a restricted area allowing for some degree of free movement or in an open space. In the latter case, a leash of approximately 2 m in length restricted movement. The high incentive was a piece of dry beef liver (0.4 to 0.6g), whereas the low incentive was the dog pellets usually eaten by the dog (0.4 to 0.6g). Preliminary observations with choice tests between liver and a variety of chow pellet foods indicated that the dogs preferred the liver. A choice between a new chow pellet and the usual chow pellet indicated that the new one was preferred, whereas the usual food was the least preferred.

Incentives were placed in a container located on a tall table. The container was visible to the animals, but out of reach. All trials were videotaped with a Sony DCR TRV 310 camera. The person taping the trial was located behind and to a side of the experimenter, so as to be able to film the direction of the dog's gaze and head. Each session involved the dog, the experimenter, and the person operating the camera.

Dogs were randomly assigned to Groups H (high incentive,  $n = 7$ ) and L (low incentive,  $n = 6$ ). During a single habituation session lasting 3 to 5 min, dogs were brought to the location within their homes where training was to take place. The experimenter called the dogs by their name and actively sought physical contact. Dogs received three units of either liver or food pellets, depending on their assigned condition, directly from the hand of the experimenter.

Immediately after the habituation session, dogs received eight preshift trials of differential reinforcement of gazing at the experimenter. Each trial lasted 2 min with an intertrial interval of approximately 2 min. Preshift trials started with the experimenter standing by the food container and calling the dog by its name just once. Dogs were reinforced every time they gazed at the experimenter with either liver or food pellets, depending on the group. Starting on the second trial, dogs were required to gaze at the experimenter for at least 1 s before receiving a reward. Usually, dogs moved their gaze from the experimenter's face to her hand as

soon as the experimenter reached for the food. A new reinforcer was delivered when the dog turned back its gaze to the experimenter's face for 1 s. At the end of each trial, the experimenter withdrew to a different location, out of the dog's visual field, while the dog remained in the training area. All the dogs in this experiment responded to their name and gazed at the experimenter at least four times during each of the final four trials (Trials 4 to 8). After the last preshift trial, dogs were removed from the training location into another area where they could move freely approximately for 1 hr.

In preparation for postshift trials, dogs were moved back to the training area. There were four trials, 2-min each, carried out under the same conditions described above for preshift trials, except that all dogs received food pellets as the reinforcer. In a final trial, dogs received again their preshift incentive (liver or food pellets). This test was introduced to control for possible effects of satiety or fatigue on behavior.

Five dependent measures were scored from videotapes during the course of the trial. Because these behaviors occurred while the animal was in contact (visual or physical) with the incentive, they could all be considered part of the consummatory repertoire.

**Food rejection (continuous sampling; Trials 8 to 13).** Number of food items rejected in a given trial divided by the total number of food items offered in a given trial. A food item was considered rejected when the dog gazed at the experimenter, the experimenter offered the food, and the dog failed to accept or eat the reward.

**Gaze duration(s).** This behavior was scored on Trials 1 to 13 by manually calculating (with a stop watch) the cumulative duration of visual contact of the dog with the trainer.

**Experimenter approach (one-zero sampling every 5 s; Trials 8 to 13).** The dog's position was classified as either "near" the experimenter if it was within half a meter from the experimenter or "far" if it was more than half a meter from the experimenter.

**Position (one-zero sampling every 5 s; Trials 8 to 13).** Classified as seated, standing, or lying down.

**Orientation (one-zero sampling every 5 s; Trials 8 to 13).** Three subcategories were scored depending on the orientation of the dog relative to the experimenter. **Experimenter:** Dog remains oriented toward the experimenter with its body and head, independently of its gaze direction. **Side:** Dog orients toward a side, relative to the experimenter, independently of its gaze direction. **Back:** Dog orients its body and head away from the experimenter, independently of its gaze direction, showing its back. When body and head were oriented differentially, the position of the head determined how orientation was categorized.

Interobserver agreement for all measures combined was above 90%. For food rejection ( $k = 1.00$ ), experimenter approach ( $k = 0.99$ ), position ( $k = 1.00$ ), and orientation ( $k = 0.98$ ), reliability was calculated on a 6 of the 13 subjects using Cohen's kappa procedure. Pearson's coefficients of correlation were calculated for gaze duration for all the dogs ( $r_s > 0.92$ ,  $N_s = 13$ ,  $p_s < .001$ , two-tailed). Analyses of variance were used except when the scores violated normality. In the latter case, the results were analyzed using Mann-Whitney nonparametric tests. In all cases, the alpha value was set at the .05 level. All analyses involved two-tailed tests.

## Results

Figure 1 shows the proportion of food rejected by the dogs in both conditions during Trials 8 to 13. Clearly, food rejection increased in dogs exposed to the incentive downshift, while remaining stable and low in unshifted dogs. During the downshift phase, dogs frequently approached and sniffed the food and immediately turned their heads and withdrew without eating it. Mann-Whitney tests indicated nonsignificant differences in food rejection across groups for Trials 8 (preshift) and 13 (test),  $Z_s < 1$ ,  $p_s < .83$ , but significantly more rejection for the downshifted dogs than the unshifted dogs on each of the four postshift trials,  $Z_s > 2.13$ ,  $p < .04$ .

Figure 2 depicts the average cumulative gaze duration during each of the 13 trials of the experiment. During preshift trials, dogs in the preferred incentive condition gradually increased gaze duration above the level of the dogs exposed to the less preferred incentive. The overall means for the 8 preshift trials were 23.1 s ( $SEM = 3.9$ ) and 15.7 s ( $SEM = 2.1$ ) for the downshifted and unshifted groups. Despite this apparent difference, a Group  $\times$  Trial analysis indicated nonsignificant effects for the interaction,  $F(7, 77) = 2.05$ ,  $p < .06$ , as well as for the two main effects,  $F_s < 2.54$ ,  $p_s < .72$ . During the postshift trials, gaze duration diverged for the two groups, decreasing for dogs exposed to the downshift, while increasing for the unshifted dogs. This pattern yielded a significant interaction between groups and trials,  $F(3, 33) = 4.36$ ,  $p < .02$ . None of the main effects were significant,  $F_s < 2.48$ ,  $p_s < .68$ . A one-way analysis on the last postshift trial (Trial 12) indicated that downshifted dogs were gazing significantly less than unshifted dogs,  $F(1, 11) = 7.95$ ,  $p < .02$ . However, when the original incentive conditions were reinstated on Trial 13, this difference was no longer detectable,  $F < 1$ .

Three major behavioral categories were scored during Trials 8 to 13 to determine the extent of the changes induced by incentive downshift. In each category there were two or three mutually exclusive behavioral components, for a total of eight individual behavioral components. Each component was analyzed with a Mann-Whitney test for each trial. The results are summarized in Table 2.

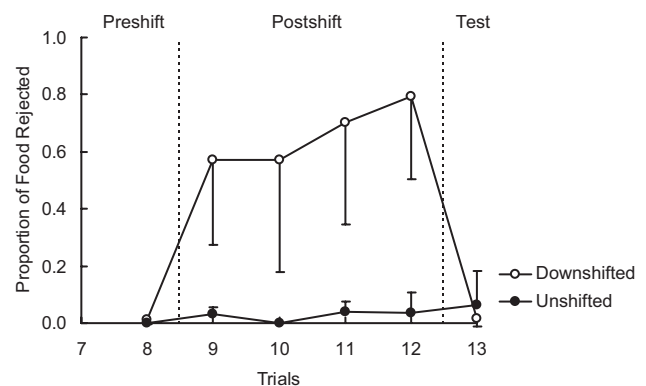


Figure 1. Proportion of food rejected during Trials 8 to 13 by dogs in each group. This measure was calculated as the ratio of items rejected to total food items offered. The dotted lines indicate a transition in incentive quality (mean  $\pm$  95% confidence interval).

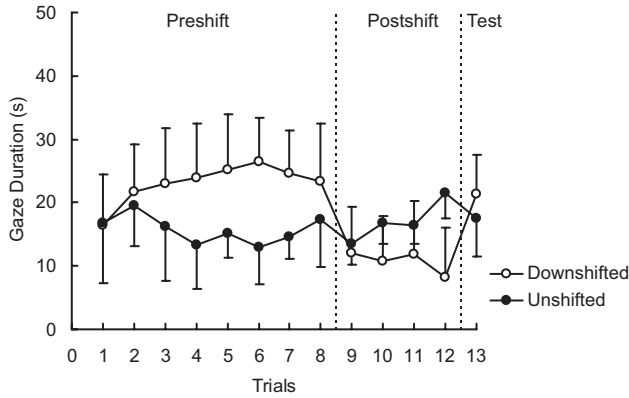


Figure 2. Gaze duration during each trial for each group. Dogs were required to gaze at the trainer for 1 s to receive food. The dotted lines indicate a transition in incentive quality (mean ± 95% confidence interval).

In terms of experimenter approach, downshifted dogs showed less “near” behavior than nonshifted dogs on Trials 11 and 12,  $Z_s > 2.10$ ,  $p_s < .04$ . A group difference in the opposite direction was also detected on Trial 13 when the preshift conditions were reinstated,  $Z = 2.03$ ,  $p < .05$ . Nonsignificant differences were found on Trials 8 to 10,  $Z_s < 1.73$ ,  $p_s > .08$ . Downshifted dogs were also significantly more likely to be far from the experimenter than unshifted dogs on Trial 11,  $Z = 2.18$ ,  $p < .03$ , but not on any

of the other trials,  $Z_s < 1.71$ ,  $p_s > .09$ . Notice that these two measures, near and far, were not strictly equivalent, with the former being more sensitive in detecting group differences than the latter.

In terms of *position*, downshifted and unshifted dogs were not different from each other in any of the three components: seat, stand, and lie down,  $Z_s < 1.86$ ,  $p_s > .06$ .

In terms of *orientation*, (a) downshifted dogs were less likely to orient toward the experimenter than unshifted groups on Trials 11 and 12,  $Z_s > 2.14$ ,  $p_s < .04$  (other comparisons were nonsignificant,  $Z_s < 1.60$ ,  $p_s > .13$ ); (b) less likely to show their back to the experimenter only on Trial 13,  $Z = 2.03$ ,  $p < .05$  (other comparisons were nonsignificant,  $Z_s < 1$ ,  $p_s > .36$ ); and (c) more likely to be at the side of the experimenter on Trial 12,  $Z = 2.51$ ,  $p < .02$  (other comparisons were nonsignificant,  $Z_s < 1.87$ ,  $p_s > .06$ ).

Discussion

These results provide the first demonstration of SNC in domestic dogs. The effect appeared in terms of food rejection as well as in terms of an interspecific communicative response (gaze direction) and postural response patterns. It is noteworthy that downshifted dogs refused to accept or consume a reward that they would readily accept and consume under almost any other set of circumstances. This phenomenon is similar to that observed in other species. Rodents, marsupials, and human babies also reject a devalued sucrose solution in a situation in which they have previ-

Table 2  
Mean and SEM Frequency of Eight Behaviors Scored on Trials 8 to 13

Groups	Trials					
	Preshift 8	Postshift 9	Postshift 10	Postshift 11	Postshift 12	Test 13
	<i>M (SEM)</i>	<i>M (SEM)</i>	<i>M (SEM)</i>	<i>M (SEM)</i>	<i>M (SEM)</i>	<i>M (SEM)</i>
Experimenter approach: Near						
Downshifted	22.72 (1.1)	19.29 (1.8)	16.14 (3.5)	13.21 (3.8)*	14.86 (4.0)*	24.00 (0.0)*
Unshifted	22.00 (1.2)	22.67 (0.7)	23.50 (0.3)	23.25 (0.8)*	23.83 (0.2)*	22.67 (0.8)*
Experimenter approach: Far						
Downshifted	1.00 (1.0)	4.71 (1.8)	7.57 (3.5)	10.79 (3.8)*	9.00 (4.1)	0.00 (0.0)
Unshifted	1.83 (1.2)	1.33 (0.7)	0.33 (0.3)	0.75 (0.8)*	0.17 (0.2)	1.00 (0.7)
Position: Seat						
Downshifted	8.14 (4.0)	6.79 (3.3)	4.57 (2.6)	3.71 (2.4)	2.00 (2.0)	2.71 (2.7)
Unshifted	8.00 (4.3)	7.50 (3.9)	9.83 (4.5)	8.83 (4.3)	8.17 (3.8)	6.83 (3.4)
Position: Stand						
Downshifted	11.86 (4.5)	16.07 (3.6)	10.86 (4.1)	10.00 (3.7)	5.14 (2.4)	14.43 (4.6)
Unshifted	11.83 (4.7)	16.50 (3.9)	10.17 (4.5)	11.17 (4.5)	10.50 (4.6)	10.67 (4.5)
Position: Down						
Downshifted	3.71 (3.4)	1.14 (1.1)	8.29 (4.1)	10.29 (3.8)	16.71 (3.6)	6.86 (4.4)
Unshifted	4.00 (4.0)	0.00 (0.0)	3.83 (3.8)	4.00 (4.0)	5.33 (4.0)	6.17 (4.1)
Orientation: Experimenter						
Downshifted	21.72 (1.3)	14.57 (2.7)	13.07 (2.9)	9.21 (2.7)*	8.50 (3.2)*	21.14 (2.0)
Unshifted	15.67 (3.2)	17.67 (1.8)	16.33 (3.0)	18.08 (2.1)*	19.17 (1.7)*	16.50 (3.2)
Orientation: Back						
Downshifted	0.86 (0.9)	1.36 (0.6)	3.36 (3.0)	1.64 (1.4)	0.29 (0.2)	0.00 (0.0)*
Unshifted	1.50 (1.0)	1.08 (0.5)	3.42 (1.7)	1.83 (1.1)	0.83 (0.5)	2.33 (1.3)*
Orientation: Side						
Downshifted	1.14 (0.5)	8.07 (2.3)	7.29 (2.5)	13.14 (3.2)	15.07 (3.1)*	2.86 (2.0)
Unshifted	6.67 (2.7)	5.25 (1.6)	4.08 (1.5)	4.08 (1.4)	4.00 (1.5)*	4.83 (2.1)

Note. Pairwise comparisons between downshifted and unshifted groups.  
\*  $p < .05$ .

ously received a sweeter solution (Kobre & Lipsitt, 1972; Mustaca, Bentosela, & Papini, 2000; Papini, Mustaca, & Bitterman, 1988). Under these conditions, the rejection of an incentive has traditionally been taken as evidence of the violation of an expectancy leading animals to forego a low-value reward when a high-value one is anticipated (e.g., Brosnan & de Waal, 2003). Unlike in these studies with mammals, experiments with goldfish (*Carassius auratus*) demonstrate a reverse SNC effect—goldfish continue to consume the less preferred food even after the downshift (Couvillon & Bitterman, 1985).

Dogs also increased gaze duration directed at an unfamiliar person (i.e., the experimenter) when this person was paired with access to food. Moreover, gaze duration was longer when the experimenter provided the more preferred food (dry beef liver) than when the food was less preferred (dog pellets). The surprising reduction in incentive quality led to SNC effect consistent with what others have described in analogous experiments with other mammalian species (see Papini, 2006).

The nature of the behavioral changes observed in this experiment is consistent with the hypothesis that the incentive downshift manipulation was accompanied by an aversive emotional state. Animals moved away from the experimenter and the source of the devalued food, orienting their body and head toward the side of the experimenter. These responses are analogous to the behaviors reported during extinction, in the same task (Bentosela et al., 2008) and in similar studies with other mammalian species, in situations that do not involve social interaction (Papini & White, 1994). The aversiveness of incentive downshifts is suggested by several lines of evidence in other mammalian species (see Papini & Dudley, 1997), including the acquisition of escape behavior from sites associated with incentive downshift in rats (Daly, 1974), the attenuation of SNC by anxiolytic treatment in mice (Mustaca, Bentosela, et al., 2000), and the increased levels of plasma cortisol in pigs (Dantzer, Arnove, & Mormede, 1980).

The present results were atypical in that the animals were observed under their usual living conditions. Most, if not all, studies of SNC have been done under the more controlled, but also more restricted conditions of laboratory research. These and previous results on the effects of omission contingencies and extinction training (Bentosela et al., 2008) represent an initial attempt at evaluating the impact of incentive changes on human–dog communication patterns. It is expected that these studies will help characterize processes of social cognition in relation to human–dog co-evolution (Milgram, Head, Weiner, & Thomas, 1994).

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