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EFFECTS OF WHITE AND INFRARED LIGHTING ON APOMORPHINE-INDUCED PECKING IN PIGEONS

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Abstract

The present experiment was concerned with the role of environment in the production and form of apomorphine-induced pecking of pigeons. Previous literature has suggested that the pecking occurs even when pigeons are placed in complete darkness, but there are no systematic or quantitative reports of such pecking. Six pigeons were tested with doses of 0.1, 0.3, and 1.0 mg/kg apomorphine. Tests were made in conditions of white and infrared light. The apparatus employed novel force transduction measures that provided for both the detection of a peck as well as its peak forcefulness. At the lowest dose tested, apomorphine elicited pecking when the pigeon was placed in white light, but not when the dose was examined under infrared lighting. As the dose increased, however, pecking was observed regardless of lighting condition. No differences were found in forcefulness of pecking as a function of lighting condition or dose. Though response output was seemingly unaffected by the lighting condition at higher doses, videotaped analysis revealed important changes in the formal characteristics of pecking. In white light, apomorphine elicited pecking at stimuli in the chamber (e.g., screw heads or the pigeon's own toes), whereas in infrared light pecking was directed at the floor directly in front of the pigeon. Such differences may be attributable to shifts in control to other stimulus modalities when vision is limited. Additionally, apomorphine may have direct effects on retinal dopamine function modulating the expression of pecking in the dark.

Keywords

Apomorphine; Stereotypy; Infrared light; White light; Force; Pigeon; Peck

Dopaminergic compounds have been shown to elicit stereotyped patterns of behavior in several species (Deliuss, 1985; Ellenbroek & Cools, 2002; Ridley, 1994). There has been some debate about the degree to which the expression of such behavior reflects a motor effect disassociated from environmental input, or an over exaggerated response to environmental stimulation. For example, Stevens, and colleagues for example, examined sensory deprivation on stereotyped "head scanning" (i.e., repetitive, side-to-side head movements, cf. Ellinwood & Kilbey, 1975) elicited by repeated administration of 1.0 mg/kg *d*-amphetamine in cats. Deafening the cats did not affect the stereotypy, but when blindfolds were placed over the eyes, the stereotypy was attenuated (Stevens et al, 1977). The authors

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suggested that the attenuation following the removal of visual stimulation implicated visual feedback as important in the expression of the behavior.

Subsequent findings, however, have not always supported such an interpretation. Konopacki (1986), for example, failed to find any attenuating effect of visual deprivation on the head scanning stereotypy induced by 2.0 mg/kg *dl*-amphetamine. When cats were placed in complete darkness, the stereotypy continued. Konopacki (1986) suggested that the stereotyped movements were due to dysregulation of motor output rather than disruption of visual stimulation, and that the attenuation reported by Stevens et al. (1977) may have been due to the restrictive nature of the blindfolds used.

Other unexplored procedural differences may be responsible for the different outcomes in past studies. Stevens et al. (1977) used a lower dose, 1.0 mg/kg, and a different form of the drug, *d*-amphetamine as opposed to the racemic form used by Konopacki (1986). So at the very least, there may be important dose issues to consider when evaluating the role of visual stimulation on drug-induced stereotypy. One goal of the present experiment was to explore further dose-environment interactions in the control and expression of pecking of pigeons induced by the direct dopamine agonist apomorphine (APO).

When given to pigeons, APO induces bouts of stereotyped pecking, which are often directed toward small, visually contrasting stimuli in the environment (Acerbo & Delius, 2004; Delius, 1985; Deviche, 1984; Goodman, 1980). The total number of pecks has been shown to be dose-dependent (Godoy et al, 2000), and with repeated administration sensitization often develops to APO's ability to induce pecking (Delius, 1985; Godoy & Delius, 1999). Interestingly, Delius (1985) mentioned that pigeons continued to peck following APO administration even when placed in total darkness. He did not, however, provide any quantitative measures of pecking in darkness (e.g., rate or force) for purposes of comparisons with pecking when pigeons could see.

In searching the literature more broadly, we could find no published data quantifying APO's effects on pecking when the pigeon is deprived visually. Additionally, there has been no description of the formal characteristics of the pecking stereotypy when, and if, it occurs in darkness. Because pigeons are highly dependent on vision for survival (cf. Güntürkün, 2000) and because the majority of research on APO-induced pecking indicates that pecks are under control of visual stimuli in the environment, apomorphine-induced pecking makes an ideal candidate to study further the role of environmental stimulation in the expression and maintenance of stereotyped behavior. Given that the pecking stereotypy appears under such strong control of visual stimuli, it seems unlikely that pecks occurring under conditions of limited or no vision would retain the same characteristics as pecks occurring when the pigeon can see. To evaluate pecking under different conditions of visual stimulation, we filmed pigeons under both white light conditions and under infrared (IR) lighting.

In addition to videotape analysis of the pigeons, we employed novel force-transduction measurements to measure the forcefulness of pecks. As discussed above, the rate of APO-induced pecking increases with dose but it is not known if there are systematic changes in other characteristics of the response. Pecking in pigeons is not a unitary response. There are several functional classes of pecks associated with food and water procurement, aggression, operant, and adjunctive behavior (Delius, 1985; Jenkins & Moore, 1973; Staddon, 1977). Changes in response output following different doses of APO may reflect a shift or emergence of different functional classes of pecks, which would likely be reflected in pecking force in addition to pecking rate.

METHOD

Subjects

Six male homing pigeons (Double “T” Farm, Glennwood, IA) were approximately 1.5 years old at the start of the experiment. Each pigeon was maintained at 85% of its free-feeding weight; a weight that approaches the normal weights of healthy pigeons in the wild (Poling, et al., 1990). Additionally, food deprivation allowed us to control feeding and crop loading in relation to drug administration; a desirable circumstance given APO’s emetic effects (e.g., Cheng & Long, 1974). Water and health grit were continuously available in the home cage. Weights were maintained via daily post-session feedings. Each pigeon had participated in several pilot experiments on effects of cocaine and apomorphine prior to conducting this experiment, and so were not drug-naïve. All procedures were approved and conducted within the ethical guidelines set at the University of Kansas.

Apparatus

The experimental chamber was a force-plate actometer (Fowler et al., 2001). The actometer was a load plate (28 cm × 28 cm) constructed from ploycarbon fiberboard. Each corner of the load plate rested upon an isometric force-transducer (Model 31a, Sensotec, Columbus, OH). Voltages from the transducers were amplified and read by a Labmaster™ board (Scientific Solutions, Mentor, OH) connected to a Pentium-class computer. Data collection software written in Free Pascal was programmed to read from each transducer at 100 samples/s. Raw data from the transducers were stored for later analysis.

The enclosure about the plate was made of clear acrylic and was spaced 1 mm above, and not touching, the surface of the plate. The ceiling of the enclosure was 22 cm from the force plate. A CCD-type board camera (VC-103, Circuit Specialists, Mesa, AZ) was located 35 cm away from one wall of the chamber, placed at a level 8 cm above the chamber floor. The camera was linked to a VCR to record each pigeon’s movement during daily sessions. Videotape was later digitized into MPEG-2 format with commercial software.

It was possible to illuminate the chamber with white light via a 75-W fluorescent bulb mounted above the chamber, parallel to the wall facing the camera. Infrared illumination was provided by an array of twenty-five 880 nm IR LED’s (QED123-ND, Digi-Key, Thief River Falls, MN). The values of the LED’s were selected based on spectral sensitivities indicating that pigeons should not be able see at such wavelengths (Bowmaker, 1977, 1991). Our pilot work provided some support that pigeons could not see, or at least could not see well. Under the IR light, for example, the birds failed to peck at grain thrown about the chamber floor, something they did readily under white light. LED’s were soldered onto a circuit board such that they were arranged in a 5 × 5 matrix, the total array was 15 cm × 15 cm. The IR source was mounted directly over the chamber.

Procedure

Each pigeon completed several pilot experiments examining the effects of APO and cocaine prior to the present procedures. In total, six weekly doses ranging from 3.0 – 10.0 mg/kg cocaine had been tested; the last dose was given six months prior to the present procedure. APO was given closer to the present study, in total 10 doses ranging from 0.1 – 1.0 mg/kg had been tested over a period of six weeks. The last pilot experiment, prior to the present experiment, was a series of three biweekly exposures to 1.0 mg/kg APO in white and IR light. So, exposure to the chamber under either white light or IR light was not novel for any pigeon.

Three weeks were interposed between the last pilot experiment and the present experiment. The present experiment consisted of a within-subject test of different doses of APO and its vehicle. Tests with APO were made in 4-day blocks. The first two days were tests in the white light; the second two days were tests in the IR light. Tests with vehicle always preceded tests with APO. Thus, during a block of tests the first day began with a test of vehicle under white light, followed on the second day by a test of APO under white light, followed on the third day by a test of the vehicle under IR light, and finally on the fourth day the dose of APO was retested under IR light. Doses were tested in ascending order across blocks; doses tested were 0.1, 0.3, and 1.0 mg/kg APO.

Prior to each session, each pigeon's weight was recorded. Injections of the vehicle or APO were made immediately prior to the bird's placement in the actometer. Data collection began approximately 15 s after placing the bird in the chamber, which allowed the pigeon to settle prior to recording from the force plate. Sessions lasted for 20 minutes. Once sessions were completed, the pigeon was removed from the chamber and returned to its home cage.

Drug Administration Procedures

APO hydrochloride (Sigma, St. Louis, MO) was dissolved into a solution of 0.1% ascorbic acid in physiological saline, which served as the vehicle. Solutions were prepared newly everyday, approximately 1 hr prior to experimentation. APO was given *im* into the pigeon's breast muscle at a volume of 1 mL/kg. The injection site alternated between the left and right breast across days in order to minimize bruising. Dosages are expressed in terms of the salt.

Data Analysis

To examine data from the force plate, recordings from each of the four transducers were summed across corresponding samples, providing a time series record of force oscillations throughout a single session. The mean of the time series, which was equivalent to the pigeon's weight, was found and then removed from the series. The time series were then filtered to find pecks. Our definition of pecks arose out of our pilot work and reports in the literature on the duration and forcefulness of pigeons' pecks (e.g., Rilling et al., 1970). Eventually, our definition identified pecks as any event that exceeded 80 g and returned to subthreshold forces (< 10 g) within 30 ms. Thus, pecks would be seen as brief, forceful events in the waveform record. For each identified peck, the peak of the waveform provided a measure of peak forcefulness of the peck. Our pilot work indicated that our algorithm would allow us to discriminate pecks from other activities, such as walking or grooming, which are characterized by different durations and waveforms. Finally, pecks were counted over several videotapes ($n = 12$) by one of the experimenters (JWP) and the correspondence between the numbers given by the analysis software and the experimenter's count was close ($r = .90$). Additional graphics and statistical analysis were performed with SigmaPlot™ (Ver. 9, Systat Software, Inc., San Jose, CA) and Systat™ (Ver. 11, Systat Software, Inc., San Jose, CA).

RESULTS

Figure 1 shows the number of pecks obtained as a function of dose of APO under different lighting conditions for each pigeon. To accommodate the variability obtained across doses and pigeons, the data have been log-transformed. Counts were adjusted by 1 prior to taking the logarithm, so zero represents the absence of pecking. When tested under white light, pecking increased with increasing dose of APO. Similarly, pecking also increased with increasing doses under IR light, yet the functions were shifted down compared to those obtained in the white light. No pigeon pecked at the lowest dose when tested under the IR

light; however, three pigeons made occasional “air pecks” (i.e., pecks not contacting a surface and forcefulness below our criterion for inclusion as a peck); but for the majority of the session pigeons simply stood, near motionless. As dose increased, however, complete and consistent pecks emerged, and at the testing of the highest dose there was no apparent difference between counts under different lighting conditions.

Repeated-measures ANOVA conducted on the log-transformed rate data revealed significant main effects of dose ($F(2,10) = 55.9$, $p < .0001$) and lighting condition ($F(1,5) = 37.6$, $p < .002$), and a significant interaction ($F(2,10) = 5.59$, $p < .025$). Follow-up Tukey HSD comparisons revealed a significant effect of lighting at the 0.1 mg/kg dose, but not at higher doses.

The peak forcefulness of pecks did not vary systematically with either APO dose or lighting condition. Figure 2 shows peak force as a function of APO for each lighting condition. Under the white light, peak force monotonically increased or increased and then decreased with increasing dose of APO. Tests under the IR light did not reveal systematic changes in the function. No data point was obtained when the 0.1 mg/kg dose was tested under the IR light as no pecking occurred.

Although the present data indicated that lighting condition played little role in the rate of pecking under higher doses of APO or the forcefulness of pecks, the similarity in number belies important differences in the formal characteristics of pecks. Analysis of the video obtained from each session revealed stark differences in the topography of pecking. Some stills from the tapes have been singled out for presentation in Figure 3. The images taken from the tests with vehicle (white light only) are meant to show that the pigeons maintained a standing position during those tests and rarely moved; similar effects were seen when vehicle was tested under the IR light.

In contrast, when 1.0 mg/kg APO was administered under the white light, pecks appeared under the control of various stimuli located in the chamber. Bird 3, for example, pecked a small screw-head located on the inside wall of the chamber, a topography shared with Birds 1, 2, and 6 (data not shown); Birds 1 and 6 additionally pecked the floor below the screw. Two pigeons (Birds 4 & 5) pecked their feet, and a representative image is shown of B4 in Fig. 3. Although the topography of stereotyped pecking varied across individuals, the topography was unchanged by dose of APO. That is, pigeons that pecked the screw head (or their own toes) emitted only that form during tests of APO.

When APO was examined under IR light, the topographies, when pecking occurred, changed in all pigeons. First, most pigeons initially engaged in bouts of “air pecking” which lasted 10–30 s. As mentioned previously, “air pecks” were strikes out into space that did not land on any surface. “Air pecking” was never observed when APO was tested under white light. At doses greater than 0.1 mg/kg, all birds transitioned from “air pecking” to pecking the chamber floor directly in front of the feet. It is important to note that pigeons were not pecking their feet under the IR light. The neck was straight and elongated rather than curving under the chest, and pecks struck the floor clearly in front of the feet, as shown in the representative images presented in Figure 3.

DISCUSSION

The APO-induced pecking of pigeons was dependent upon the lighting condition. At the lowest dose of APO tested (0.1 mg/kg), pecking was directed at visual stimuli in the chamber (screwheads or the pigeon’s own toes), but under the IR light there was no pecking. The data from the tests with the lowest dose are consistent with those of Stevens et al. (1977), who concluded that visual stimulation was important in the control of amphetamine-

induced “scanning” stereotypies observed with cats. As dose increased, however, pecking occurred in both the white light and IR conditions – a finding consistent with Konopacki’s (1986) report that higher doses of amphetamine elicited stereotyped responding in cats placed in total darkness. Our findings also confirm Delius’ (1985) report that APO induces pecking in conditions when the pigeon (presumably) can not see. Thus, the data reveal an important interaction between the dose of APO and visual stimulation on the number of elicited pecks. At low doses, the occurrence of pecking appears dependent on visual cues, but at high doses pecking occurred regardless of lighting conditions.

The use of the force-plate also allowed us to investigate changes in forces of pecks under different conditions. Previous data has indicated multiple functional key peck classes may be emitted by pigeons (e.g., Delius, 1985; Jenkins & Moore, 1973), and a consistent change of force with dose may have indicated a transition from one class of pecks to another. At this point, however, our data provide no evidence of differences in forcefulness of pecks across either lighting or dose conditions. It is important to note, however, that our sampling rate of 100 Hz allowed detection of pecks, but not finer quantification of the force dynamics of each peck. There may remain important changes in the force waveforms of different pecks that would not be reflected in peak force.

The similarities in the response to higher doses of APO across lighting conditions should not be taken to mean that there were no differences between pecking under white and IR light. Videotapes analyses revealed that the formal characteristics of pecking were changed across the different conditions. Under visual deprivation, pecks were directed at the floor immediately in front of the pigeon. Although such responding could be taken as evidence of direct motor effects uncoupled from sensory feedback, we would argue that such a conclusion is premature because other stimuli could have served a controlling function for the response. Deprived of visual stimulation in a sound-attenuated chamber, the primary sensory stimulation left to the pigeon would be tactile stimulation from the chamber floor, and all pigeons uniformly showed floor-directed pecking in the dark under higher doses of APO. So, it is possible that pecking was controlled in part by tactile stimulation from the floor. Of course, once pecking began, acoustic feedback could have served as an additional maintaining source of control, as it may serve in normal feeding (cf. Delius, 1985). Thus, we suggest that even when the pigeon can not see well, APO-induced pecking may still be stimulus-governed, though the source of control shifts from visual stimulation to other available modalities.

Although changes in controlling stimuli help understand the final topography taken by pecking, additional variables will need to be sought to supply a full account of induced pecking, especially its initial emergence. One interesting possibility may lie in effects of APO in the visual system. Acerbo and Delius (2004), for example, have suggested that APO may produce interoceptive cues in the retina that may play a role in the response to APO. In birds, dopamine is produced in the amacrine cell layer and is diffusible to all retinal cells where it is involved in many functions, including light transduction, circadian linked processes, ganglion cell activity, and neurotrophic functions (Djamgoz & Wagner, 1992). Dopamine transmission seems particularly important in the enhancement of cone function and suppression of rod function, effects critical to its role in light-adaptation (Witkovsky, 2004). Normally, cone function would be suppressed after the pigeon is placed in the dark, but it may be that APO, via its direct effects on dopamine receptors, continues to facilitate cone function and interfere with normal dark adaptation. Such effects in the retina could continue to provide stimulation similar to that present in the light, and thus facilitate pecking in the dark.

Finally, APO-induced pecking of pigeons may be an overlooked vehicle for modeling repetitive movement disorders. Several lines of non-human experimentation have advanced the current knowledge of many functional aspects of repetitive movements and stereotypy (cf. Eilam & Szechtman, 2005; Lewis et al., 2007; Ridely, 1994). Although rodents are the most widely used animals in models of repetitive movement disorders, avians have particular features that may make them especially suitable for study (Garner, Meehan, & Mench, 2003). In regard to the effects of APO in pigeons, pecking is an easily measured response that occurs at a high rate (e.g. 100–150 pecks/min). Also, as mentioned earlier, avians subsist primarily through vision, as do most humans. So, birds may provide for direct experimentation of visually controlled stereotypy in a manner not possible with rodents (see Geary & Akins, 2007 for similar arguments related to drug seeking behavior).

In particular, the present findings demonstrate that at low doses of APO, pecking depends on visual stimulation from the environment, while at higher doses pecking occurs even when the pigeon can not see. Such a finding may correspond to varying degrees of severity in the stereotypy of humans where mild forms of stereotypy may be eliminated using simple environmental manipulations, but extreme or excessive stereotypy persists, or is transformed, in attempts to eliminate it. With respect to the latter case, the use of the IR light could be seen as an attempt to “block” the response, only to have it re-emerge in a different topography (e.g., pecking the floor). Similar transformations in topography have been observed in reaction to blocking extreme forms of stereotypy and self injury in humans (cf. Lovaas et al 1987). Thus, the dose-response relationship between APO and pecking may serve as a useful domain to explore environmental manipulations on visually controlled stereotypy along a dimension of severity.

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Figure 1.

The effects on lighting condition on the apomorphine-induced pecking. The vertical axis plots the logarithm of the number of pecks against different doses of apomorphine on the horizontal axis. The number of pecks was adjusted by 1 so that log could be taken in cases when no pecks occurred. Open circles represent data taken from determinations made in the white light; filled squares represent corresponding data obtained from tests under the IR light.

Figure 2.

The effects of lighting condition on the peak force of pecks. Median forces are plotted on the vertical axis against dose of apomorphine on the horizontal axis. Details are the same as in Figure 2.

Figure 3.

The effects of lighting condition on response topography are shown for select conditions (columns) for two different pigeons (rows). The left column shows images taken following a test of the vehicle under the white light. The middle column shows images taken from tests of 1.0 mg/kg apomorphine made in the white light. The right column shows images taken from a replication of 1.0 mg/kg apomorphine made under the IR light.