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Evaluating an Animal Model of Compulsive Hoarding in Humans

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Recently, researchers have begun to advocate use of an animal model for understanding compulsive hoarding in humans. Nevertheless, a comprehensive review of the literature for this argument is lacking. We compare data for compulsive hoarding behavior in humans with hoarding in several vertebrates (rat, bird, and primate) to examine the potential validity of an animal model of hoarding. Although the strength of each animal model varies, there is provisional evidence in support of an analogue between hoarding in nonhuman animals (especially rodents) and humans, most notably on neurobiological grounds. Nevertheless, substantially more evidence is needed before this relationship can be confirmed with confidence. We identify gaps in the literature and offer suggestions for further investigation of the validity of animal models of human hoarding.

Keywords: hoarding disorder, compulsive hoarding, comparative psychology, animal hoarding

Hoarding behavior in humans is broadly defined as acquiring and failing to discard items without, or of limited, value (Frost & Gross, 1993). Hoarding is characterized by ambiguous definitional criteria, prompting the recent proliferation of studies devoted to refining its diagnostic status for the *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.; *DSM-5*; American Psychiatric Association, in press; e.g., Mataix-Cols et al., 2010). Hoarding is marked by poor treatment response and a chronic and unremitting course (Frost, Steketee, & Williams, 2000; Grisham, Brown, Savage, Steketee, & Barlow, 2007). In addition, hoarding often causes grave threats to the health and safety of sufferers due to the vermin, mold spores, lack of sanitation, and precariousness of debris in the home environment that characterize this condition (Frost & Gross, 1993; Frost, Steketee, & Williams, 2000; Kim, Steketee, & Frost, 2001; Thomas, 1998). Moreover, among all anxiety disorders, hoarding has perhaps the highest association with work and social disability (such as occupational and role impairment; Tolin, Frost, & Steketee, 2007) and the highest rates of comorbidity with other disorders (Frost, Steketee, & Tolin, 2011; Frost, Steketee, Williams, & Warren, 2000b; Leckman, Mataix-Cols, & Rosario-Campos, 2005; Wheaton, Timpano, LaSalle-Ricci, & Murphy, 2008). Together, these factors underscore the necessity for an improved understanding of clinical hoarding.

To improve pharmacological, and perhaps psychological, interventions, many researchers have sought links between hoarding symptomatology and its accompanying neurobiology (An et al., 2009). Animal models have contributed a great deal of knowledge to other disorders in humans by highlighting salient pathological and phenotypic features that are mimicked in animals. Successful examples of this approach include depression (e.g., McKinney & Bunney, 1969), schizophrenia (e.g., Green, 1983; McKinney & Moran, 1981), obsessive–compulsive disorder (OCD; e.g., Pitman, 1989), and substance use and abuse (e.g., Koob & Volkow, 2010). As a consequence, if a valid animal model for hoarding were discovered, it would have the potential to provide similarly helpful insights. Many researchers (e.g., An et al., 2009; Mataix-Cols, de la Cruz, Nakao, & Pertusa, 2011; Preston, 2011; Tolin, Kiehl, Worhunsky, Book, & Maltby, 2009) have linked hoarding behaviors in humans to similar behaviors in other animals, and some have urged the need for a comprehensive review of the commonalities and differences in these cross-species comparisons.

The purpose of the present review is to critically evaluate the validity of an animal model for understanding clinical hoarding in humans by comparing extant data on behavioral, neuroanatomical, biochemical, and genetic bases for hoarding across species and to determine which animal species, if any, display hoarding behaviors most relevant to human hoarding. Such a review is justified by the proliferation of studies suggesting parallels (especially in etiology) between the hoarding behaviors of humans and animals, the evidence of which has yet to be systematically evaluated. The first step in the explication of any model system is to establish an analogy, which is characterized by congruence between variables that are causally related from two different domains (Overmier & Patterson, 1988). Hence, we limit our review to an evaluation of evidence for analogy rather than homology, the latter of which requires a clear demonstration of shared evolutionary origins (Wall & Shani, 2008). In the case of animal and human hoarding, such a demonstration is largely lacking.

A further consideration for the review relates to the general consensus in the field that any model system should satisfy criteria for predictive validity (in which human and model exhibit parallel responses in course and outcome, as well as to similar interventions) and construct validity (in which the condition in human and model may be explained by similar underlying processes) as

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primary objectives (for further discussion of these criteria, see Overall, 2000). At first glance, it may appear that the discrepancy in items typically hoarded by humans (inedible objects) and animals (food items) would present a significant impediment to meeting these criteria. Nevertheless, although a successful material analogy requires correspondence between sets of variables in two domains, this correspondence, as Overmier and Patterson (1988) suggested, does not need to be superficially identical. Furthermore, we will present exceptions to this trend throughout the article (e.g., humans who hoard food and animals that hoard inedible objects), especially in the case of rodents and birds. More importantly, we present construct validity for the model in the form of etiologic parallels for hoarding in humans and animals as well as similarities in the presentation (if not always the net result) of the acquisitive and storing behaviors. Furthermore, we present predictive validity for the model in the form of preliminary evidence revealing parallels in response to pharmacological interventions. We begin our review by exploring the phenotype of hoarding in humans and animals in greater detail.

Hoarding in Humans

Hoarding in humans is characterized by a compulsion to acquire and save items of limited value (e.g., old newspapers and clothes), as well as an inability to discard these items. Such hoarding results in generally unmanageable amounts of clutter (Frost & Gross, 1993), often leading to significant impairment, distress, or both (Gilliam & Tolin, 2010). Clinical hoarders save items for reasons varying from imbuing objects with personal significance to the desire to delay difficult decisions about discarding materials perceived as potentially useful (Mataix-Cols et al., 2010).

Although officially listed as one of the eight symptoms of obsessive–compulsive personality disorder (OCPD) in the *Diagnostic and Statistical Manual of Mental Disorders* (4th ed., text rev.; *DSM–IV–TR*; American Psychiatric Association, 2000), most researchers identify hoarding as a distinct symptom or subphenotype of OCD (Frost, Krause, & Steketee, 1996; Shafran & Tallis, 1996; Torres et al., 2012), a pathology noted for its clinical and etiologic heterogeneity (Wendland et al., 2009). Furthermore, Frost, Steketee, and Tolin (2012), Mataix-Cols et al. (2010), Mataix-Cols and Pertusa (2012), and Pertusa et al. (2010) are among those who have suggested or proposed hoarding as a separate, but related, disorder from OCD in *DSM-5* (American Psychiatric Association, in press), and Mataix-Cols et al. (2010) advocated a new diagnosis called “hoarding disorder.” Proposed criteria for hoarding disorder in the *DSM-5* were further discussed by Tolin (2011), as shown in Table 1.

Criteria typically used to distinguish hoarding from other disorders are threefold: (a) acquiring/difficulty discarding objects[1]; (b) hoarded material takes up most of the living space; and (c) significant distress, reduced functioning, or both, as a consequence of hoarding (Frost & Hartl, 1996; Grisham et al., 2007). More extensive diagnostic criteria for hoarding have been suggested by Steketee and Frost (2003), and include (a) clutter takes up most of the home; (b) difficulty discarding items; (c) current or past compulsive acquiring (e.g., excessive buying/collecting items that are not needed, are not affordable, or both); (d) clutter causes distress, impaired functioning, or both; (e) clutter persists for at least 6 months; and (f) hoarding behaviors are not better accounted for by another mental disorder, like dementia or major depressive disorder (MDD).

Hoarding in Animals

A wide variety of animal species hoard, including such mammals as marsupials, insectivores, primates, carnivores, rodents, and lagomorphs; such birds as raptors, woodpeckers, and perching birds; and such insects as beetles, ants, wasps, and bees (Vander Wall, 1990). Although equivalent to terminology used for humans, hoarding in the animal behavior literature has been variously described as handling food to conserve it for future use (Vander Wall, 1990) or transporting objects (such as food pellets) from the living space or “home” cage to another location (Manosevitz & Lindzey, 1970; Ross, Smith, & Woessner, 1955).

In addition to the confusion created by using the term “hoarding” for both humans and animals without sufficient evidence that they are analogous, the term’s clarity is obscured within the animal literature by its interchangeable use with the terms *caching*, *storing*, or both (Power, 1990; Stephens, Brown, & Ydenberg, 2007; Vander Wall, 1990). Hoarding in animals is generally measured by the frequency and amount of food that is stored (e.g., in a laboratory setting, hoarding is measured by the number of food pellets stored within the home cage during a specified period of time; Manosevitz & Lindzey, 1967, 1970). Similarly, articles adopting such terms as “object retrieval” (Wallace 1997a, 1997b, 2001) add to confusion in the nomenclature. Furthermore, the natural history and ecological conditions for hoarding in animals are poorly understood, in part because the literature is scattered across various taxonomic groups (Vander Wall, 1990).

Researchers have described two criteria that must be met for behavior to be classified as hoarding in animals: postponing food consumption, and the special handling of food for conservation (Vander Wall, 1990). However, hoarding by animals encompasses a diverse range of behaviors, including the amount and type of material stored, the amount of time between storing and consumption, the location and number of food stores, and the purpose of the food storage (e.g., personal consumption or nourishment for offspring). Common distinctions within hoarding include short- versus long-term hoarding (i.e., how long the food is stored before usage), as well as *scatter* and *larder* hoarding, whereby the former category encompasses having multiple hoarding sites over the home range and the latter category encompasses having one predominant hoarding site (Male & Smulders, 2007; Power, 1990; Smith & Reichman, 1984). However, some researchers dispute the status of these variables as categorical, viewing them as end points of a continuum (Stanback, 1990).

Much of the hoarding data on animals in the 20th century was dominated by experimental methodology on rodents (Manosevitz & Lindzey, 1970), with lab conditions often characterized by closed alleys with a home cage at one end and a food bin at the other (Ross et al., 1955). Classical variables investigated in rodents included determining the emotional and learning conditions under which hoarding occurred or the analysis of factors (e.g., various light and food availability conditions) that increased or decreased

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[1] In more recent research (e.g., Gilliam & Tolin, 2010), this category has been further subdivided into excessive acquiring and failure to discard possessions, leading to four elements as opposed to the three outlined here.

Table 1
Proposed DSM-5 (American Psychiatric Association, in press) Criteria for Hoarding Disorder as Shown in Tolin (2011)

A. Persistent difficulty discarding or parting with possessions, regardless of the value others may attribute to these possessions.
B. This difficulty is because of strong urges to save items and/or distress associated with discarding.
C. The symptoms result in the accumulation of a large number of possessions that fill up and clutter active living areas of the home or workplace to the extent that their intended use is no longer possible. If all living areas are uncluttered, it is only because of the interventions of third parties (e.g., family members, cleaners, authorities).
D. The symptoms cause clinically significant distress or impairment in social, occupational, or other important areas of functioning (including maintaining a safe environment for self and others).
E. The hoarding symptoms are not due to a general medical condition (e.g., brain injury, cerebrovascular disease).
F. The hoarding symptoms are not restricted to the symptoms of another mental disorder (e.g., hoarding due to obsessions in obsessive–compulsive disorder, decreased energy in major depressive disorder, delusions in schizophrenia or another psychotic disorder, cognitive deficits in dementia, restricted interests in autism spectrum disorder, food storing in Prader–Willis Syndrome).

Specify if
With excessive acquisition: If symptoms are accompanied by excessive collecting or buying or stealing of items that are not needed or for which there is no available space.

Specify whether hoarding beliefs and behaviors are currently characterized by
Good or fair insight: Recognizes that hoarding-related beliefs and behaviors (pertaining to difficulty discarding items, clutter, or excessive acquisition) are problematic.
Poor insight: Mostly convinced that hoarding-related beliefs and behaviors (pertaining to difficulty discarding items, clutter, or excessive acquisition) are not problematic despite evidence to the contrary.
Absent insight: Completely convinced that hoarding-related beliefs and behaviors (pertaining to difficulty discarding items, clutter, or excessive acquisition) are not problematic despite evidence to the contrary.

hoarding (Stellar, 1943). Toward the latter half of the 20th century, investigations turned toward relations between food storing and memory in birds, as well as the genetic foundations of food hoarding in honey bees.

Psychological Models of Clinical Hoarding in Humans

Early models of hoarding-type behaviors included Freud's (1908) theory of the *anal triad*[2] (miserliness, orderliness, and obstinacy), which purportedly resulted from overly harsh toilet training in the anal psychosexual stage, or Fromm's "hoarding" characterological type, which referred to individuals who derived security from collected objects (Grisham & Barlow, 2005).

Current theories of clinical hoarding are dominated by the cognitive–behavioral model, which views hoarding as characterized by information-processing deficits, including decision-making errors and category underinclusiveness, the latter of which describes the tendency to assign unique, specific properties to objects that would normally be subsumed under the same general category (Gilliam & Tolin, 2010; Tolin, Villavicencio, Umbach, & Kurtz, 2011). As viewed from the perspective of the cognitive–behavioral model, hoarding is marked by difficulties in forming interpersonal relationships and emotional attachment, behavioral avoidance, and distorted beliefs about objects. (Ayers, Wetherell, Golshan, & Saxena, 2011; Frost & Gross, 1993; Frost & Hartl, 1996; Frost, Steketee, & Green, 2003; Gilliam & Tolin, 2010; Melamed, Szor, Barak, & Elizur, 1998; Muroff, Bratiotis, & Steketee, 2011; Saxena & Maidment, 2004; Shafran & Tallis, 1996; Steketee & Frost, 2003; Tolin et al., 2007; Wheaton, Abramowitz, Franklin, Berman, & Fabricant, 2011). Controlled studies corroborating the utility of this model reveal cognitive deficits, such as slower information processing and spatial attention, as well as category underinclusiveness and slowed reaction times (RTs; Grisham et al., 2007; Wincze, 2001). Other data point to delayed verbal recall and impaired organization in individuals with primary hoarding symptoms (Hartl et al., 2004).

Nevertheless, patients with hoarding symptoms have generally shown poor responses to cognitive–behavioral treatment compared with other OCD subphenotypes (Abramowitz, Franklin, Schwartz, & Furr, 2003; Abramowitz, Wheaton, & Storch, 2008; Mataix-Cols, Marks, Greist, Kobak, & Bauer, 2002; Saxena, 2007), which could indicate problems with the underlying theory. Alternatively, these findings may cast doubt not on the theory itself as much as the malleability of deficits in clinical hoarders.

Evidentiary Basis for Comparisons of Hoarding in Humans and Animals

Although claims that the underlying causes of hoarding are similar in humans and animals have begun to accumulate (e.g., An et al., 2009; Anderson, Damasio, & Damasio, 2005; Kellett, 2007; Mataix-Cols et al., 2011; Tolin et al., 2009), data for such claims have yet to be organized into a systematic review.

Human Data on Hoarding

To evaluate the validity of an animal model of hoarding, we first present evidence including behavioral, neurobiological, biochemical, and genetic findings from the human literature.

Human data on hoarding: Behavioral evidence. Hoarding behaviors occur early in life. Data from Leckman and colleagues (2005) indicate an age of 25 to 27 months for the onset of behaviors analogous to hoarding, such as the collection and storage of objects (Evans et al., 1997). Many researchers have suggested an early age of onset for the presence and/or formal diagnosis of hoarding (Ayers, Saxena, Golshan, & Wetherell, 2010; Jefferys & Moore, 2008), such as late childhood or early adolescence (Frost & Gross, 1993). Symptom severity appears to increase with age

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[2] Although this terminology has mostly faded from psychological parlance, a recent review by Haslam (2011) shows its persistence (and arguably, its descriptive validity) under other labels.

(Ayers et al., 2010; Grisham, Frost, Steketee, Kim, & Hood, 2003), which may partially explain why individuals with hoarding generally do not present for treatment until later in life (Saxena, 2007).

Among OCD subphenotypes, individuals with hoarding symptoms have an earlier age of onset (Abramowitz et al., 2008). Higher rates of hoarding are found among older populations (Steketee et al., 2001), with particularly high rates among elderly women (Marx & Cohen-Mansfield, 2003). However, these findings may at least partly reflect the co-occurrence of hoarding and dementia (Stein, Laszlo, Marais, Seedat, & Potocnik, 1997), particularly of the frontotemporal variety (Nakaaki et al., 2007). Studies sampling multiple age groups have shown that the majority of hoarding cases occur in persons younger than 65 years of age (Halliday, Banerjee, Philpot, & Macdonald, 2000). Additional data show that hoarding preceded by trauma generally results in a later age of onset than hoarding without traumatic precedent (Grisham & Barlow, 2005). Other age data reveal a similar age of onset for clutter and difficulty discarding symptoms, whereas symptoms of acquiring generally begin later in life (Grisham et al., 2005).

Data on sex differences in hoarding are equivocal. Among geriatric populations, women evidence higher rates of hoarding (Hurley, Scallan, Johnson, & De La Harpe, 2000; Klosterkötter & Peters, 1985; Marx & Cohen-Mansfield, 2003). In one study, women who hoarded tended to have greater symptom severity and higher comorbidity compared with men who hoarded (Wheaton et al., 2008). However, other findings suggest that males have higher rates of hoarding than females (Samuels et al., 2002; Samuels, Bienvenu, Grados, et al., 2008), and still other data (e.g., Labad et al., 2008) show no gender differences. The reasons for these discrepancies require clarification.

As a result of its associated cognitive deficits, hoarding behavior is often characterized by a repetitive urge to acquire and store items, as well as difficulty in discarding items perceived as having either informational use or value (e.g., periodicals) or sentimental value (Frost, Hartl, Christian, & Williams, 1995). Furby's (1978) classification of hoarding as instrumental (saving items with use value) versus sentimental (saving items with emotional value) helps clinicians identify the type of objects hoarded and the appropriate treatment. For example, the treatment of instrumental saving can be focused on challenging distorted underlying beliefs about the perceived utility of these objects. In contrast, the treatment for sentimental saving can be focused on problems in relationship formation and emotional attachment. One other type of object hoarded by humans deserves special note because of its comparability to items typically hoarded by animals, that is, food. Some researchers have documented rare cases of human food hoarding (Barocka et al., 2004), and still others have described the everyday behavior of humans acquiring and storing food in refrigerators, freezers, and cupboards as "hoarding," (e.g., Bartness, Keen-Rhinehart, Dailey, & Teubner, 2011), consistent with the term's usage in the animal behavior literature to describe adaptive, normative behavior among hoarding species.

Most individuals who hoard live in social isolation (Montero-Odasso et al., 2005). Most are unmarried (Frost & Gross, 1993; Kim et al., 2001), and many stay inside their homes and keep others from entering because of embarrassment or fear of having their items purged by outsiders (Wincze, 2001). Furthermore, individuals who hoard are usually characterized by low levels of insight into their behavior (Abramowitz et al., 2008; Frost et al., 1996; Greenberg, 1987; Hahm, Kang, Cheong, & Na, 2001; Nakaaki et al., 2007; Saxena, 2007; Steketee & Frost, 2003; Storch et al., 2007; Wincze, 2001). When questioned about their motivation, hoarders often cite their fear of throwing something away that might be needed for future use (akin to instrumental saving; Warren & Ostrom, 1988). Therefore, hoarders typically postpone the decision-making process, citing their fear of losing a part of themselves or someone they love symbolized by the object (akin to sentimental hoarding; Wincze, 2001).

Though epidemiological data on hoarding were, until recently, virtually nonexistent (Frost, Steketee, & Williams, 2000; Saxena, 2007), studies over the past few years suggest that as much as 5% of the population display compulsive hoarding (Gilliam & Tolin, 2010; Mataix-Cols et al., 2011; Samuels, Bienvenu, Grados, et al., 2008), with some estimates at high as 5.8% (Timpano, Exner, et al., 2011). Some lifetime estimates are as high as 14%, according to data from the National Comorbidity Survey Replication (Grisham & Norberg, 2010; Ruscio, Stein, Chiu, & Kessler, 2010). Additionally, compulsive hoarding appears to be a cross-cultural phenomenon, based on evidence for hoarding behaviors from such countries as the United States, the United Kingdom, Australia, Italy, Germany, and Japan (Bloch, Landeros-Weisenberger, Rosario, Pittenger, & Leckman, 2008; Mataix-Cols et al., 2010). Some studies (Dong, Simon, & Evans, 2012; Dong, Simon, Mosqueda, & Evans, 2012) have shown differential rates of hoarding based on income and ethnicity. For example, African American adults with lower levels of education and income showed higher rates of hoarding than Caucasian adults; however, broader sampling strategies and further studies are required before interpreting these findings with confidence.

Human data on hoarding: Neurological evidence. Results from neuropsychological tests have revealed memory impairment in compulsive hoarders as evidenced by diminished performance on the Rey-Osterrieth Complex Figure Test (RCFT; Osterrieth, 1944), as well as the short and long-delayed recalls of verbal information on the California Verbal Learning Test (CVLT; Delis, Kramer, Kaplan, & Ober, 1987; Grisham et al., 2007; Hartl et al., 2004). Furthermore, difficulties on the Affective Go/No-Go, Intra-Extra Dimensional Set Shift, and Stockings of Cambridge subtests of the Cambridge Neuropsychological Test Battery (CANTAB; Sahakian & Owen, 1992) reveal impairments in executive skills, such as categorization, cognitive set-shifting, and planning abilities, respectively (Grisham, Norberg, Williams, Certoma, & Kadib, 2010). Evidence for general impairment in information categorization and organization (Wincze, Steketee, & Frost, 2007), planning (Grisham et al., 2007; Hartl et al., 2004), error monitoring (Mathews, Perez, Delucchi, & Mathalon, 2012), and especially impaired decision-making capabilities (Bechara, Damasio, Damasio, & Anderson, 1994; Grisham et al., 2007; Lambrecq et al., 2009; Lawrence et al., 2006; Nakaaki et al., 2007; Tolin et al., 2011, 2012; Tolin & Villavicencio, 2011), have also been found in numerous studies. Additionally, shared features between hoarding and attention-deficit/hyperactivity disorder (Hartl, Duffany, Allen, Steketee, & Frost, 2005) further implicate impaired executive functioning in hoarding, corroborated by a study from Grisham and colleagues (2007), in which hoarding participants demonstrated impairment on measures of response inhibition, sustained attention, and spatial ability. Other studies have documented attentional problems in hoarding, such as greater impulsivity and impaired detection of target stimuli (Koby et al., 2008; Meunier, Tolin, Frost, Steketee, & Brady, 2006).

Nevertheless, the presence of executive functioning deficits among hoarders is equivocal, as other studies have shown a lack of executive impairment measured by such neuropsychological tests as the Wisconsin Card Sorting Task, the Stroop test, and the Trail Making Test, as well as by neuroimaging studies demonstrating dorsolateral prefrontal cortex (DLPFC) integrity (Nakaaki et al., 2007; Volle, Beato, Levy, & Dubois, 2002). Nakaaki and colleagues (2007) hypothesized that the Iowa Gambling Task (IGT) may be more sensitive to the kinds of cognitive deficits seen in hoarding (e.g., impaired decision making), a finding corroborated in pilot data (An et al., 2009), and studies by Tolin and colleagues (2012) as well as Blom and colleagues (2011).

Although a plethora of imaging studies for OCD phenotypes are available, recent evidence suggests that these data may not be applicable to such OCD subphenotypes as hoarding (An et al., 2009; Mataix-Cols et al., 2003, 2004; Saxena, 2008). Saxena (2008) as well as An and colleagues (2009) asserted that hoarding and OCD are distinct not only because of genotypic differences but also because of symptoms unique to hoarding, such as the compulsion to acquire and save, difficulty discarding, indecisiveness, perfectionism, procrastination, disorganization, and avoidance. This distinction may account for discrepant findings in the OCD literature. For example, whereas a decrease in gray matter (GM) volume was noted for OCD participants in the frontal gyrus (Pujol et al., 2004) and left frontotemporal, left dorsolateral prefrontal, superior temporal, medial temporal, inferior temporal, pericentral, parahippocampal, and insular regions (Kwon, 2004), other studies (e.g., Valente et al., 2005) have shown increased GM in many of these areas in OCD participants. One study specific to hoarding showed decreased GM volume in BA6, the premotor cortex and supplementary motor area (Gilbert et al., 2008), and Perry et al. (2012) showed decreased GM volume in the bilateral globus pallidus, left putamen, and lateral temporal lobe in patients who presented with a behavioral variant of frontotemporal dementia and hoarding. Nevertheless, because other obsessive–compulsive behaviors were present in these patients (Perry et al., 2012), it is difficult to isolate differences specific to hoarding. These and other findings, such as the hypometabolism in the orbitofrontal cortex (OFC), caudate nuclei, and thalamus, as well as lower activity in the cingulate cortex observed in hoarding compared with nonhoarding OCD patients (Saxena, 2004), suggest the importance of separating hoarding from other OCD subphenotypes.

In the first brain imaging study of hoarding (Mataix-Cols et al., 2003), normal volunteers ($n = 10$) evidenced unique brain activations in response to hoarding stimuli in a symptom provocation paradigm. While in the scanner, four 6-min experiments were performed in which test subjects were exposed to 50 aversive color pictures and 50 neutral color pictures selected from the International Affective Picture System (Lang et al., 1997), as well as additional color pictures related to each of three symptom types of OCD (washing-related, checking-related, and hoarding-related). Compared with both the normally aversive and symptom-related aversive pictures for washing and checking, normal controls showed specific brain activity in ventral prefrontal, limbic, cerebellar, visual, and, to a lesser extent, DLPFC areas in response to hoarding-aversive pictures (Mataix-Cols et al., 2003). Although this study set up a comparative basis for areas of the brain relevant to hoarding-like stimuli in normal populations, it is not clear whether these findings can be generalized to the clinical population in question. In particular, the brain areas responsible for hoarding stimuli in normal populations may be qualitatively distinct from those in clinical hoarders.

A more recent imaging study achieved this task by testing both normal and clinical populations, using the same symptom-provocation paradigm (An et al., 2009). Activations to hoarding-related stimuli among a group of normal controls ($n = 21$) were compared with activations among a group of OCD patients with predominant hoarding symptoms ($n = 13$), and a group of OCD patients without hoarding symptoms ($n = 16$). All three groups showed increased frontolimbic activity in response to hoarding stimuli, including the anterior ventromedial prefrontal cortex (VMPFC), medial temporal structures, thalamus, and sensorimotor cortex. However, OCD patients with predominant hoarding symptoms showed greater activation in the bilateral anterior VMPFC than either healthy controls or the OCD group without hoarding symptomatology. Therefore, this study, as well as that of Mataix-Cols et al. (2003), reveals ventral prefrontal activity in response to anxiety-based hoarding stimuli in normal populations, supporting the hypothesis of differential brain activations among hoarding compared with other OCD subphenotypes. Additionally, these studies yield data specific to clinical populations of hoarders (i.e., greater VMPFC activation among hoarding OCD patients compared with normal controls and other OCD symptom types). These studies therefore provide evidence for a conceptualization of hoarding as continuous with normal behavior as suggested by Preston, Muroff, and Wengrowitz (2009), similar to the characterization of certain individuals as nonclinical “pack rats” (e.g., Luchian, McNally, & Hooley, 2007). In such conceptualizations, VMPFC activity is associated to some extent with hoarding across various populations, and it is only when significant hyperactivation in the VMPFC appears that pathological, clinical instances of hoarding ensue.

Some of the earlier data on hoarding neuroanatomy were inferred from lesion analyses of patients demonstrating hoarding behavior or “pathological collecting.” In one case study of a patient who hoarded toy bullets, imaging revealed damage to the left OFC and caudate (Hahm et al., 2001). The OFC has also been implicated in a case study of pathological collecting behavior, whereby activation in the polar prefrontal cortex (PFC) was also detected (Volle et al., 2002). This activation correlated with the patient’s pathological collecting behavior. Furthermore, Anderson and colleagues (2005) showed mesial PFC activation in pathological collectors compared with nonpathological collectors. They speculated that the hoarding behaviors of both humans and nonhuman animals were mediated by subcortical areas (e.g., the striatum and thalamus), and that the difference between hoarding in animals and clinical hoarding in humans was accounted for by dysregulation of cortical circuitry (especially the medial PFC [mPFC]; Anderson et al., 2005). In review of these and other studies, Mataix-Cols and colleagues (2011) concluded that the anterior ventromedial prefrontal and cingulate cortices have been consistently implicated in both organic hoarding (i.e., hoarding resulting from brain pathology) and nonorganic hoarding (i.e., hoarding behaviors in the absence of brain pathology), which may suggest that the neurological pathways to different types of hoarding are similar.

These studies of pathological collecting may not be directly comparable because of threats to construct validity inherent in discrepant measurement, especially because recent data suggest that hoarding differs from normal collecting behaviors (Nordsletten & Mataix-Cols, 2012). Nevertheless, Wang, Seidler, Hall, and Preston (2012) showed OFC involvement specific to hoarding behaviors, which may suggest some overlap in the neural correlates of hoarding and collecting behaviors. Future studies in which pathological collecting is the construct of interest should incorporate more rigorous diagnostic criteria, as well as standardized measures, to determine the overlap between pathological collecting and hoarding.

Additional data specific to hoarding in which frontal cortical activations were demonstrated showed activity in the left precentral/superior frontal gyrus (BA4/6), left fusiform gyrus (BA37), and right OFC (BA11; Mataix-Cols et al., 2004). Results also showed that healthy controls demonstrated greater activation than hoarding patients in bilateral visual areas (BA7/19), and the authors speculated that this may have been due to controls paying more attention to the visual cues in the pictures used in the symptom-provocation paradigm and less to the emotional salience of the pictures (Mataix-Cols et al., 2004).

Tolin et al. (2009) found that hoarding participants ($n = 12$) displayed hemodynamic activity in the left amygdala and parahippocampal gyrus, extending into the thalamus and left cerebellum as well as the lateral OFC during decision-making about whether to keep or discard items in the scanner compared with 12 healthy controls. Control participants displayed more hemodynamic response in the right lingual gyrus than hoarding participants during the task. Furthermore, decisions to keep rather than discard items in the hoarding participants were associated with greater activity in the superior temporal gyrus, middle temporal gyrus, medial frontal gyrus, anterior cingulate cortex (ACC), precentral gyrus, and cerebellum. In other words, areas notable for their association with decision-making and response inhibition seem to be activated by hoarding, assuming that symptom provocation paradigms are a valid indicator of clinical hoarding.

However, these findings contradict those of Saxena and colleagues (Saxena, 2008; Saxena et al., 2004), who showed decreased glucose metabolism in the right posterior cingulate cortex, the right dorsal ACC, the bilateral putamen, and the cuneus compared with healthy controls and in the dorsal ACC when compared with nonhoarding OCD patients. The authors suggest that this discrepancy may stem from biphasic neural patterns in hoarding patients, who display decreased activity at rest but increased activity in these regions during decision making (the activity of which was absent in the Saxena et al., 2004, study; Tolin et al., 2009). The authors argue that their research is consistent with rodent data underscoring the roles of the ACC (e.g., de Brabander, de Bruin, & van Eden, 1991), hippocampus (e.g., Kolb, 1977), and globus pallidus (e.g., Mogenson & Wu, 1988). Other human research consistent with these data include the loss of GM in the globus pallidus (Perry et al., 2012), as well as hippocampal dysfunction associated with hoarding symptoms in studies by Melamed and colleagues (1998) and Luchins (1990).

Most recently, evidence for the role of the ACC in hoarding emerged in a study by Tolin et al. (2012), in which participants with hoarding disorder ($n = 43$) showed significant abnormal activation patterns in both the ACC and the insula in response to decisions of whether to discard objects compared with normal controls ($n = 33$). Because the ACC is involved in response conflict, these findings—perhaps not surprisingly—suggest that clinical hoarders are more emotionally conflicted about discarding objects than are nonclinical individuals. One primate study (Stern & Passingham, 1994) has also implicated the ACC (and the nucleus accumbens [NAcc]) in a group of monkeys, which is discussed in a later section.

Variation in specific brain loci associated with hoarding may be the product of one or more of any number of factors, including differences in measurement, provocation paradigms, construct variability (e.g., hoarding vs. pathological collecting), and variability in symptom presentation (sentimental vs. instrumental saving), highlighting the need for more precise operationalization and standardization of hoarding, as well as standardization of experimental stimuli. Comorbidity may also contribute to discrepant findings, as hoarding is rarely seen in isolation. Thus, continued work in this area is recommended to isolate effects specific to hoarding disorder.

Human data on hoarding: Biochemical evidence. Although few studies have examined the biochemistry associated with hoarding, Melamed and colleagues (1998) speculated that hoarding reflects the failure of the hippocampus to modulate the impact of mesolimbic dopaminergic activity on the NAcc, resulting in a disinhibition of stereotypical behaviors. Other support for the role of dopamine in hoarding derives from studies by Saxena and Rauch (2000) and Stein and colleagues (1997), who found that dopamine antagonists decreased hoarding in humans.

Another study of cerebral metabolic patterns in compulsive hoarding found lower glucose levels in the posterior cingulate gyrus and cuneus compared with normal controls, as well as lower activity in the cingulate cortex (Saxena et al., 2004). These findings parallel an earlier case study revealing glucose hypometabolism in the OFC associated with hoarding (Hahm et al., 2001).

There is also evidence for an effect of stimulants on hoarding, perhaps reflecting the tendency of stimulants to induce stereotypies (Mason, 1991). For example, a small amphetamine dosage resulted in increased hoarding behavior in one study. Nevertheless, the effects of stimulants may be dose-dependent; in another study, a larger dosage eliminated hoarding (Kaplan & Hollander, 2004). Furthermore, another case study showed the effectiveness of stimulant medication for hoarding, specifically for reducing the procrastination associated with the disorder (Kaplan & Hollander, 2004). Saxena (2007) theorized that stimulants can aid functioning in the medial prefrontal areas associated with attention and executive functioning, perhaps underlying their effectiveness in treating hoarding.

Many studies (Abramowitz et al., 2008; Black et al., 1998; Hahm et al., 2001; Lambrecq et al., 2009; Luchian et al., 2007; Mataix-Cols et al., 1999, 2003; Saxena et al., 2002; Winsberg, Cassic, & Koran, 1999) show that selective serotonin reuptake inhibitors (SSRIs) are ineffective for hoarding. These findings may imply that serotonin is unlikely to be the predominant neurotransmitter involved in hoarding, although drawing inferences about etiology from medication response is fraught with numerous conceptual difficulties (Ross & Pam, 1995). Saxena (2007) recommended that future clinical trials for hoarding focus on non-SRI medications such as stimulants (as also suggested in Kaplan & Hollander, 2004), antiglutmatergic agents (especially in light of findings from Wendland & colleagues, 2009, implicating a glutamate transporter gene in hoarding), and cognitive enhancers such as donepezil or galantamine, which facilitate cholinergic transmission in the cerebral cortex (Gaston, Kiran-Imran, Hassierm, & Vaughn, 2012). Clearly, much more work is needed to elucidate the role of neurotransmitters in hoarding.

Human data on hoarding: Genetic evidence. As mentioned earlier, hoarding is a strongly heritable phenotype that is genetically distinct from other forms of OCD (Saxena, 2008). Notably, hoarding appears to be the most heritable OCD subphenotype (Samuels, Bienvenu, et al., 2007; Saxena, 2007). Some studies have revealed that 84% to 85% of hoarding patients reported at least one first-degree relative as a "pack rat," (Frost & Gross, 1993; Winsberg, Cassic, & Koran, 1999); however, it is unclear whether genetic factors, shared environmental factors, or both, are responsible for this aggregation. Furthermore, although one twin study has shown the contribution of both genetic and nonshared environmental factors for compulsive hoarding, genetic factors substantially outweighed environmental factors, accounting for 50% of the variance (Iervolino et al., 2009). Molecular-genetic studies have also pointed to a genetic influence on compulsive hoarding (Lochner et al., 2005; Samuels, Shugart, et al., 2007; Timpano, Schmidt, Wheaton, Wendland, & Murphy, 2011; Zhang et al., 2002); for example, Samuels, Shugart, et al. (2007) demonstrated significant linkage for compulsive hoarding to a marker on chromosome 14, which has been implicated in medical conditions ranging from mental retardation to lymphoma to Alzheimer's disease (Kamnasaran & Cox, 2002). Other findings linking hoarding to chromosome 14 (specifically 14q) were replicated the following year (Liang et al., 2008).

Timpano, Schmidt, and colleagues (2011) demonstrated that the Val/Val genotype (BDNF Val66Met) was linked to hoarding behaviors. Another study revealed that siblings concordant for hoarding evidenced significant allele sharing in the 4q34–35 (in close proximity to D4S1625), 5q35.2–35.3, and 17q25 regions (Zhang et al., 2002). In another study, Leckman and colleagues (2003) revealed recessive allele activity in hoarding, a finding corroborated by data indicating much greater recessive allele activity in OCD participants with hoarding of Afrikaner descent than either nonhoarding OCD participants or healthy controls (Lochner et al., 2005). Furthermore, Afrikaner participants with hoarding symptoms were much more likely to have the L/L genotype of the COMT Val158Met polymorphism compared with nonhoarding OCD participants and controls (Lochner et al., 2005). These findings highlight the need to test various hoarding populations for differences.

Although research from Grados and Wilcox (2007) did not analyze OCD according to subphenotype, the glutamate transporter gene, SLC1A1, has also been found in research specific to hoarding. In a large case-control study of OCD patients ($n = 325$) and sex/ethnically matched controls ($n = 662$), six single-nucleotide polymorphisms (SNPs) were genotyped (Wendland et al., 2009). Results demonstrated that SNP rs3933331, located 100 kb upstream of the SLC1A1 transcription initiation site, was linked to hoarding behavior (Wendland et al., 2009). Given robust findings linking glutamate to OCD in animal models (McGrath, Campbell, Parks, & Burton, 2000; Nordstrom & Burton, 2002), imaging studies (Rosenberg & Keshavan, 1998; Rosenberg et al., 2000), genetic studies (Arnold et al., 2004; Delorme et al., 2004), and clinical studies documenting the effectiveness of riluzole, an antiglutamatergic agent, in treating treatment-resistant OCD (Pittenger, Krystal, & Coric, 2006), its potential role in hoarding is not unprecedented. Data from Wendland and colleagues (2009) corroborate the dysfunctional role of glutamate in OCD and hoarding with mediation through SLC1A1.

Animal Data on Hoarding

Evidence from humans with compulsive hoarding will now be weighed against extant data for animal species. Substantial variability exists not only in the degree of fit for comparison of specific animal species with humans but also within animal species. Although there are a number of species that hoard, many (especially invertebrates) differ considerably from the hoarding behaviors in humans. For example, although honey bees hoard, the vast phylogenetic differences between insects and humans raises serious questions about the applicability of a honey bee model of human hoarding. In other words, it would be unwarranted to claim that the recent finding linking hormones to hoarding in humans, with marked increases in food hoarding in women during pregnancy and lactation (Bartness et al., 2011), parallels findings for honey bees of two candidate genes implicated in honey bee hoarding, PDK1 and HR 46, which relate to ovary size (Wang et al., 2009), or that the implication of memory in human hoarding relates to the finding of the contribution of the mushroom bodies (believed to be functionally related to hippocampi in humans) to hoarding in honey bees (Stephens et al., 2007). In other words, the basic physiological machinery (to say nothing of the disparate behavior and functions of hoarding in each) are so discrepant as to render comparison between hoarding in humans and such invertebrates as honey bees of questionable value. Evidence, therefore, will be constrained to vertebrates, and the order of assessment will proceed from the most to least distant of humans' evolutionary relatives.

Avian Data on Hoarding

Hoarding is common in many species of birds, probably due to fitness advantages ranging from food storage during periods of abundance to food use during periods of scarcity (Andersson & Krebs, 1978). Other fitness advantages for hoarding by birds include withdrawing food from competition (Tomback, 1978), decreasing the rate of decay in food (Smith & Reichman, 1984), and increasing reproductive success (Koenig & Mumme, 1987). The most notable bird species that hoard are parids (Brodin & Clark, 1997; Gibb, 1960; Hogstad, 1989; Kimberly & Morrison, 1990; Smulders, 1998; Suhonen, 1993), such as marsh (Clayton & Cristol, 1996; Cowie, Krebs, & Sherry, 1981; Healy & Suhonen, 1996; Shettleworth & Krebs, 1982; Sherry, 1982; Sherry, Krebs, & Cowie, 1981; Stevens & Krebs, 1986), willow (Alatalo & Carlson, 1987; Brodin, 1994a; Brodin, 1994b; Brodin & Kunz, 1997; Healey & Suhonen, 1996; Lahti & Rytkönen, 1996; Suhonen & Inki, 1992), crested (Haftorn, 1954, 1956a, 1956b, 1956c; Lens, Adrisensen, & Dhondt, 1994), coal (Brotons, 2000; Male & Smulders, 2007), and Siberian tits (Alatalo & Carlson, 1987; Pravosudov, 1986), as well as the closely related black-capped and boreal chickadees (Haftorn, 1974; Hitchcock & Sherry, 1995; Shettleworth, Hampton, & Westwood, 1995; Shiflett, Smulders, Benedict, & DeVoogd, 2003). Also renowned for hoarding are corvids (Bednekoff, Balda, Kamil, & Hile, 1997; Bennett, 1993), including nutcrackers (Balda, 1980; Balda & Kamil, 1992; Tomback, 1980; Vander Wall, 1982), crows (Power, 1990), ravens (Harriman & Berger, 1986), jays (Bossema, 1979; Bunch & Tomback, 1986), and magpies (Buitron & Nuechterlein, 1985), as well as species from the Laniidae, Muscicapidae, Strigidae, Tytonidae, Cracticidae, Picidae, Falconidae, and Sittidae families (Power, 1990). Birds vary greatly in hoarding behavior in terms of short versus long-term hoarding strategies or scatter versus larder hoarding.

Avian data on hoarding: Behavioral evidence. The few studies that have examined the topic of age in avian hoarding have yielded conflicting results. One study (Lens et al., 1994) showed increased hoarding with age in the crested tit, whereas another showed that yearlings hoard at twice the rate of adults among willow tit species (Lahti & Rytkönen, 1996). In contrast, Brotons (2000) showed no differences in adult and juvenile hoarding in coal tits. Although many behaviors, such as hoarding intensities and hoarding rates by season, are often shared among parids (Brodin, 1994a; Lens et al., 1994), age differences may differ across parid species. Similarly, there are few data on sex differences in hoarding parids, although studies suggest a lack of differences (Brotons, 2000; Lahti & Rytkönen, 1996).

Parids are characterized by long-term, scatter hoarding, in which stored food is used repeatedly within various time intervals, and conditions such as the time of day and season have discrepant effects on hoarding behavior (Brotons, 2000). Territorial and social conditions also play a role in avian hoarding, as in the willow tit's preference for solitary hoarding compared with hoarding in the context of conspecifics (Lahti & Rytkönen, 1996), or the coal tit's higher rates of hoarding when neighboring conspecifics are absent (Brotons, 2000).

Regarding the aforementioned challenge of comparing human hoarding behaviors to animal species that predominantly hoard food, it is notable that some parids, such as scrub-jays, store inedible items when food is unavailable (Grodzinski & Clayton, 2010). Presumably, the behavior is so ingrained as to persist even in the absence of food. Furthermore, numerous instances of corvids hoarding inedible objects have been documented (e.g., Emery, 2004; Bugnyar, Stöwe, & Heinrich, 2007), and some have suggested that young corvids in particular hoard inedible objects as a form of play or that corvids cache inedible objects in sight of conspecifics in order to learn about the pilfering techniques or intentions of others (van Horik, Clayton, & Emery, 2012). Finally, the behavior of male MacGregor's bowerbirds collecting colorful fruits and shiny objects to decorate their bowers has been described as hoarding in some sources (e.g., Vander Wall, 1990), and has even prompted appropriation as a term to describe the condition of hoarding in humans: The "bowerbird symptom" (Fitzgerald, 1997). However, its function as a courtship display and mating strategy in addition to the lack of research confirming its status as a legitimate, and comparable type of hoarding behavior as seen in other avian species, render it dubious for comparison with human hoarding at this point in time.

Avian data on hoarding: Neurological evidence. Neurological evidence implicates the hippocampus—known for its role in spatial orientation—in food storing by birds (Brodin, 2010). Specifically, findings reveal a positive correlation between hippocampal volume and hoarding (Sherry & Duff, 1996), as well as hippocampal activation during hoarding among avian species (Sherry & Duff, 1996; Shiflett et al., 2003). There are more hippocampal (HF) neurons in hoarding chickadees than nonhoarders (Smulders & DeVoogd, 2000), supporting the relationship between hippocampal function and hoarding in food-storing birds. Additionally, findings from Krushinskaya (1966) implicate more general involvement of the dorsomedial telencephalon (which includes the hippocampus) in food hoarding. Finally, the septum has also shown involvement in food hoarding among parids (Shiflett, Gould, Smulders, & Devoogd, 2002).

Avian data on hoarding: Biochemical evidence. The only data related (obliquely) to biochemical correlates of food hoarding in birds suggest increased hippocampal neurons in food-hoarding birds compared with nonhoarding birds, the number of which increases in autumn—the season with the largest number of food items cached (Smulders et al., 2000; Smulders & DeVoogd, 2000).

Avian data on hoarding: Genetic evidence. One study testing cells immunopositive for three different Immediate Early Gene Products (Fra-1, c-Fos and ZENK) for the purposes of mapping neuronal activity in HF in black-capped chickadees revealed that Fos-like immunoreactive neurons correlated with the food items remembered only among food-storing birds, whereas Fra-1-like immunoreactive neurons were downregulated in food-storing birds and nonstoring birds alike. Furthermore, ZENK-like immunoreactive neurons in HF were related to the accuracy of cache retrieval (Smulders & DeVoogd, 2000). In other words, food-hoarding birds have more HF neurons than nonhoarders, and these numbers increase in autumn when large amounts of food are cached. Although without an immediately self-evident analogue for humans, if differences in hippocampal neurons were discovered between humans with and without hoarding disorder (and/or if seasonal differences in hoarding patterns were found in humans), then findings such as these may merit scrutiny.

Evaluation of the Avian Model of Compulsive Hoarding Behavior in Humans

Although there are marked differences between human and avian hoarding, the solitary, territorial traits that characterize most parids may bear similarities to the isolated, contained conditions under which humans hoard. It is also promising that there is some evidence to suggest that certain avian species (e.g., corvids and parids) hoard inedible objects, as most humans tend to hoard inedible objects over food. Furthermore, the role of the hippocampus (which is functionally homologous in avian species and humans; Shiflett et al., 2003) and the septum in hoarding behavior for both species are noteworthy, despite the seemingly opposite direction of the effect. In theory, the enlarged hippocampus found in birds that hoard may indicate behavior that is normal and adaptive (e.g., "place neurons" in birds help them retrieve food stores; Adams-Hunt & Jacobs, 2007; see Sherry & Mitchell, 2007, for further information), whereas damage to this area in humans results in hoarding behavior that is pathogenic (e.g., impairing survival, as indicated by human cases of hoarding-related fatalities). All of the genetic and neurological data on food-hoarding birds have thus far implicated hippocampal neurons as well as early gene products related to their functioning. However, in addition to anatomical differences in brain features between humans and birds, many more areas of the brain have been implicated in human than in avian hoarding. Therefore, more neurological, as well as genetic, evidence is needed to justify comparisons between hoarding in humans and birds.

Overall, the data for a plausible avian model of human hoarding are preliminary. There has been relatively little research on factors responsible for "impairment" of hoarding behaviors in birds; most research on food storage in birds has concentrated on fitness variables or neural structures (e.g., hippocampus) that mediate hoarding. Additionally, the vast majority of birds are scatter hoarders, whereas humans almost exclusively hoard material in one place, a pattern more consistent with larder hoarding. Few genetic data have been collected on avian hoarding, further limiting comparisons with humans.

Rat Data on Hoarding

In contrast, rodent data have shown more promise for comparisons of hoarding behaviors with humans. Although data have documented hoarding in many rodent species, including gerbils (Ågren, Zhou, & Zhong, 1989; Glickman et al., 1970; Nyby & Thiessen, 1980; Tsurim, Abramsky & Gettinger, 2004; Wong, 1984; Wong & Jones, 1985), mice (Barry, 1976; Chen, Wang, Wang, Zhou, & Liu, 2005; Ellison, 1996; Manosevitz & Montemayor, 1972; Pinto & Schmidek, 1994; Smith & Ross, 1953a, 1953b; Tannenbaum & Pivorun, 1984), and hamsters (Bevan & Grodsky, 1958; W. I. Smith, Krawczun, Wisehaupt, & Ross, 1954; Waddell, 1951; Wong & Jones, 1985), the preponderance of data available for rats make them the most suitable exemplar for comparison with human hoarding. Furthermore, because rats in particular have been documented hoarding inedible objects (e.g., Bartness and colleagues, 2011, claim that when wild rats do hoard, it is not food that they hoard, but rather inedible and often shiny objects), they are a particularly appropriate species for comparison with humans who, as noted previously, tend to hoard objects of the inedible variety.

Rat data on hoarding: Behavioral evidence. A variety of theories regarding the motivation or necessary conditions for rat hoarding have been tested over the years, especially in the first half of the 20th century, as have variables associated with hoarding, such as age and sex. We discuss these variables next.

Age differences. Although few in number, studies have consistently shown that hoarding tends to increase with age in the rat species (Albino & Long, 1951; Hunt, 1941; Marx, 1950a; Porter, Webster, & Licklider, 1951; Wolfe, 1939), a finding consistent with human hoarding.

Other rat hoarding data for which age was examined emerged in two groups of rats with mPFC lesions. One group had neonatal lesions of the mPFC region, whereas the other had lesions to the mPFC in adulthood (de Brabander et al., 1991). Although hoarding behavior was recovered with maturation in the neonatal group of rats, the adult rats that displayed normal hoarding behavior prior to lesions were unable to regain any prior hoarding behavior.

Sex differences. Data specific to sex differences in hoarding behavior for rats are scant. Two studies (Herberg, Pye, & Blundell, 1972; Licklider & Licklider, 1950) demonstrated sex differences in the type of material hoarded. They revealed that only female rats hoard inedible material, mirroring human hoarding, in which the predominant material hoarded is also inedible. The only other discrepancy in male and female rats is that male hoarding depends upon a hypothalamic mechanism, which is only active during nutritional depletion (whereas undeprived female rats still hoard, especially during oestrus; Herberg et al., 1972).

The few studies documenting sex differences have revealed greater amounts of hoarding activity in female rats, with one notable exception: De bruin (1988) found that male rats hoarded more in both food-present and food-deprived conditions. Otherwise, female rats hoarded twice as many pellets as males in a study by Wolfe (1939). Similarly, Morgan, Stellar, and Johnson (1943), Smith and Ross (1950), and Fleming and Brown (1975) also demonstrated increased hoarding in female rats compared with males. Marx (1950b) hypothesized that the oestrus cycle contributed to the greater frequency of hoarding in female rats, a finding comparable to food hoarding in humans, indicating a possible hormonal role in hoarding across species. However, Marx (1951) demonstrated that time mediated the effect of sex differences: Male rats hoarded more during the first 30 min of an experimental manipulation, after which females hoarded more during a 24-hr test period. Therefore, other variables (in this case, time) may moderate or mediate the relationship between sex and hoarding. Furthermore, the absence of extensive data on hormonal involvement in human hoarding (and the absence of data implicating hormonal involvement of hoarding material other than food in humans) makes this comparison speculative pending further investigation into hormonal contributions to hoarding.

A more recent study by Jenkins (2011) documents sex differences in two species of kangaroo rats. Although males for both species (*Dipodomys merriami* and *Dipodomys ordii*) evidenced more larder hoarding than females, they differed in replacement strategies for lost hoards. *Dipodomys merriami* males were less likely to replace larder hoards than females of the same species, whereas *Dipodomys ordii* males were more likely to replace these hoards than females. The authors attributed these discrepancies to differences in body size and correlated aggressive behaviors.

It is clear from the extant data that variables associated with sex differences in hoarding rats have not been isolated with certainty. Because methodological weaknesses (varying from different species of rats tested to small sample sizes) characterize the studies on sex differences in rat hoarding, more extensive data are needed before firm conclusions regarding sex differences can be drawn.

Environmental differences. In contrast, considerable work has examined the conditions under which rats hoard. For example, the effects of food deprivation on hoarding in rats have been tested repeatedly (e.g., Hunt, 1941; Morgan et al., 1941; Stellar, 1943; Wolfe, 1939). Stellar (1943) concluded that food deprivation is a necessary condition for hoarding in rats. In contrast, Bindra (1947) argued that food deprivation is neither necessary nor sufficient for hoarding because the motivation for hoarding food is the same as that for eating food (i.e., physiological conditions were equivalent for rats hoarding or eating food), a hypothesis supported by a later study (Smith, Maybee, & Maybee, 1979). Further complicating the picture are results from Smith and Ross (1953) showing that food deprivation inhibits hoarding in rats. Cabanac and Swiergiel (1989), on the other hand, found that rat starvation increased food hoarding (but not ingestion, contrary to Bindra's suggestion that the same conditions underlie both behaviors). Bartness and colleagues (2011) concluded that food deprivation is the most important factor predicting food hoarding across species, including rats, hamsters, and humans. Although most evidence suggests a connection between food deprivation and hoarding, the deprivation paradigm would benefit from further testing.

Motivation. Additional constructs that have been tested among rats are the effects of fearfulness (and the related construct of "shyness"), frustration, and aggression on hoarding behaviors. In the first case, Miller and Viek (1944) experimentally induced fear in rats through a strange-cage situation, which increased their hoarding behavior, a finding corroborated by Hess (1953) and Manosevitz (1963). This result supports a security hypothesis, whereby rats more often bring food to a place of maximum security.

Bindra's (1948) results partially corroborated this hypothesis by finding that an optimum difference in security between the home cage and the cage with the hoarded material is necessary for hoarding, and that the material hoarded must be of some value to the rat. Additionally, Bindra concluded that shyness, which he operationalized by behavioral indications of security discrepant in home cage and closed/open alley arrangements, mediated the relationship between hoarding and environmental conditions of security (Lindzey & Thiessen, 1970; Vander Wall, 1990).

In contrast, in some studies (Hunt, Schlosberg, Solomon, & Stellar, 1947; McCord, 2007), infantile frustration has been shown to lead to higher rates of hoarding in adult rats. In one study, frustration (provoked by food weaning) increased hoarding in both infant and adult rats (Albino & Long, 1951). In contrast, infantile frustration had no effect on hoarding in rats in another study (McKelvey & Marx, 1951). Similarly, the lone study to test the effect of aggression in paired fighting situations (in which a food pellet was placed between hungry rats, triggering fighting), showed no effect on hoarding (Stamm, 1955). Further research is needed to clarify the relationship between hoarding behaviors and emotions, such as aggression and frustration.

Researchers have also examined the association between social factors and hoarding in rats. In one study, rats first reared in group conditions and then habituated to individual living conditions were tested for hoarding in both group and isolated conditions. Under group conditions, the rats ate more and hoarded less, but in isolation, they ate the same amount but hoarded more (Denenberg, 1952), suggesting that hoarding competed with eating. Group characteristics have also influenced food hoarding, as in a recent study of buff-breasted rats, who hoarded more in groups with intraspecific competition than in groups of interspecific (Chinese white-bellied rats) competition (Tong, Zhang, Wang, & Lu, 2012).

More studies manipulating social conditions must be performed before conclusions can be drawn about the effect of group size on hoarding. Nevertheless, extant data suggest that group size affects hoarding behaviors, though the type and intensity of the effect require clarification. Combined with the rat data on shyness as a factor in hoarding, this information may bear important implications for the socially isolated behavior of humans who hoard compulsively. If further evidence supports the finding that rats hoard more in isolation, similar factors responsible for this behavior may help explain the socially isolated conditions under which humans hoard.

Rat data on hoarding: Neurological evidence. Some research (Kelley & Stinus, 1985; Whishaw & Kornelsen, 1993) implicates the NAcc, a brain area intimately tied to reward, as playing a key role in food hoarding behavior in rats. Kelley and Stinus (1985) argued that, in a situation conducive to hoarding, appropriate external cues in the environment (such as dispersed food pellets or the presence of novel vs. familiar environments) and internal stimuli create a motivational state in which the NAcc is activated to produce hoarding. However, the NAcc is unlikely to be the only brain area involved in hoarding. One of the essential behaviors for hoarding in rodents, acquisition, has been associated with subcortical areas, including the ventral tegmental area (VTA), lateral hypothalamus, and thalamus, as well as mesolimbic structures involved in homeostatic regulation (Anderson et al., 2005). The VTA and lateral hypothalamus, in particular, have been explicitly associated with hoarding in rats. For example, rats with small thermal lesions to the VTA hoarded significantly fewer food pellets than sham-operated rats (Stam, de Bruin, van Haelst, van der Gugten, & Kalsbeek, 1989), a finding consistent with results from de Brabander, de Bruin, and van Eden (1993). Additionally, Bentley (1966) found that damage to an area nearby to the VTA, the mammillary body, resulted in impoverished hoarding in rats.

Further corroborating data on effects of the VTA on hoarding, Stam and colleagues (1989) found that damage to the VTA resulted in a broad range of prefrontal dysfunctions and argued that damage to the mPFC disrupts hoarding behavior in rats. The connection between mPFC dysfunction and hoarding in rats also emerged in studies by Kolb (1974), Nonneman and Corwin (1981), Kelley and Stinus (1985), Kalsbeek, de Bruin, Feenstra, Matthijssen, and Uylings (1988), and de Brabander and colleagues (1991). Additionally, one of these studies (Stam et al., 1989) related impairment in rat hoarding to OFC damage, although Kolb (1973) found that lesions in the OFC did not affect hoarding. Therefore, the evidence is consistent in implicating the mPFC in hoarding in rats, but inconsistent for OFC involvement.

Both the OFC and the mPFC have been implicated in human hoarding, as discussed previously; however, direct comparison is complicated by differing types of brain data. For example, methodology in the human literature on hoarding is dominated by imaging studies, whereas methodology in the rodent literature is dominated by lesion studies. That said, lesioning of mPFC areas resulted in less hoarding in rats, a finding consistent with human data revealing correlations between pathological collecting behavior and activation of the mPFC (Anderson et al., 2005), and compulsive hoarding in another study (An et al., 2009). These data suggest that the mPFC is crucial to hoarding (or at least to cognitive functioning closely linked to hoarding, such as planning and organization) in rats and humans, whereby damage results in less hoarding and activation results in more hoarding. Nevertheless, as noted earlier, caution is urged in equating pathological collecting and hoarding.

Unlike VTA lesions in rats, lesions to the lateral hypothalamus have consistently resulted in increased hoarding behaviors in rats (Blundell & Herberg, 1973; Herberg & Blundell, 1967). In one study, lateral hypothalamic stimulation in rats increased hoarding even for satiated rats, a finding replicated by Phillips, Cox, Dakolewski, and Valenstein (1969). Additionally, food ingestion inhibited feeding but not hoarding (Herberg & Blundell, 1967). Blundell and Herberg (1973) showed that the stimulation of specific areas of the lateral hypothalamus elicited hoarding behavior even in rats with no previous hoarding behavior.

Related to these studies are findings concerning hippocampal and septal lesions in rats. Wishart, Borhman, and Mogenson (1969) found that out of three groups of rats (sham-operated control rats, rats with septal lesions, and rats with bilateral hippocampal lesions) tested under both normal feeding and deprived conditions, the most significant effects on hoarding occurred among the food-deprived group of rats with hippocampal lesions, in which food hoarding significantly increased. This result is especially important in light of the previous discussion of avian findings: Unlike cases in which hippocampal involvement facilitated hoarding in certain avian species, rats and humans show increased hoarding in response to hippocampal dysfunction, suggesting disparate mechanisms in hoarding across species, different ways of operationalizing hoarding (e.g., hoarding may be framed as an adaptation in memory, aiding survival for birds as opposed to being clinically dysfunctional for humans), or both.

Less dramatically, but still important, was the interaction between food deprivation and septal lesions, which resulted in diminished hoarding for rats (Wishart et al., 1969). The authors concluded that the hippocampus inhibits hoarding, whereas the septum facilitates hoarding, and that lesions to these areas interact with other conditions (e.g., food deprivation) to enact change in hoarding behavior. They concluded that the hippocampus and septum influence the neural mechanisms of the hypothalamus involved in food hoarding, and referred to earlier hypothalamic findings (whereby food ingestion inhibits feeding but not hoarding; Herberg & Blundell, 1967) in arguing that a neural system subserving hoarding could be distinctive from, although functionally related to, a neural system controlling feeding. Therefore, it seems that the neural area involved in the feeding system, the hypothalamus, is also involved in food hoarding, although the two can operate independently.

The anterior thalamus has also been implicated in hoarding behavior in rats; in Vanderwolf's (1967) study, hoarding behavior was depressed by lesions to the anterior thalamus and medial cingulate cortex. He hypothesized that anterior thalamic nuclei are one of the main inputs to the cingulate cortex; therefore, both areas were affected. Furthermore, Vanderwolf hypothesized that hoarding reflects a disturbance of a high level of motor control and that limbic regions may also play an important role in hoarding. The involvement of such regions may help to explain the sentimental saving variant of hoarding in humans.

Rat data on hoarding: Biochemical evidence. Dopamine, a neurotransmitter that plays a key role in the expectation of reward, has been implicated not only in human studies of compulsive hoarding but also in hoarding behavior in nonhuman animals. Rats whose hoarding behavior had been disrupted by VTA lesions were restored to normal levels of hoarding after the introduction of levodopa (Kelley & Stinus, 1985), a finding replicated by Stam and colleagues (1989). Dopamine effects specific to the mPFC were shown in another study (Kalsbeek et al., 1988), in which neonatal lesions of the VTA in rats destroyed the major part of mesocortical DA fibers that connect to the PFC, resulting in dopamine depletion connected to hoarding impairment. Furthermore, lesions to the NAcc, which result in dopamine depletion, resulted in extinction of hoarding behavior in rats in one study (Whishaw & Kornelsen, 1993). Most recently, Li and colleagues (2012) showed decreases in food foraging following haloperidol (a dopamine D2 receptor antagonist) administration. Therefore, dopamine may play a key role in rats' hoarding behavior, suggesting that this behavior may be rewarding for them.

Other neurochemicals have also been linked to hoarding. In one study, neither injections of GM1 (monosialotetrahexosylganglioside) nor the peptide ORG2766, an ACTH-(4–9) analogue, to rats with mPFC lesions restored normal food hoarding behaviors (de Brabander et al., 1993). In another study, bilateral injections of gamma-aminobutryic acid (GABA) into the subpallidal region, of haloperidol into the NAcc, and of procaine into the mediodorsal thalamus reduced hoarding in Wistar rats, whereas bilateral injections of procaine into the pedunculopontine nucleus did not. These findings point to an association between hoarding and the subpallido-mediodorsal thalamus (an area associated with memory) projections as opposed to the subpallido-pedunculopontine (an area associated with locomotion) projections (Mogenson & Wu, 1988).

Other neurotransmitters and hormones have also been implicated in food hoarding in rats. One study demonstrated that epinephrine reduced hoarding behavior in rats, whereas glucose and insulin had no effect (Stellar, 1943). Another study documented the effects of amphetamines on hoarding in animals, paralleling previously discussed results for the effect of amphetamines on hoarding in humans (Kaplan & Hollander, 2004). In this case, when rats were administered small dosages of amphetamines, their hoarding increased. However, when they received large amphetamine dosages, hoarding behavior was extinguished (Zucker & Milner, 1964), again mirroring findings in humans. The reasons for these curvilinear effects require clarification.

Sex hormones have also been shown to affect hoarding. An ovariectomy in one study resulted in increased hoarding in rats (G. H. Wang, 1923). In a later study, an ovariectomy also led to a sharp increase in the hoarding behavior of female rats, which stabilized after 5 to 6 weeks (Coling & Herberg, 1982). Additionally, the intramuscular administration of estradiol benzoate reduced hoarding activity. However, one study (Donohoe, Stevens, Johnson, & Barker, 1984) demonstrated no significant effects of estradiol (of either the beta or alpha isomer) on hoarding behavior in female rats. These discrepant findings could be due to the lack of an ovariectomy in the rats from Donohoe and colleagues (1984) or to differing dosages of estradiol.

The effect of the thyroid on hoarding behavior in rats was tested in a study in which one group of rats was fed thiouracile, a thyroid depressant, a second group was subjected to thyroidectomy, and a third group was injected with thyroxine (Stellar, 1951). No significant effect on hoarding was detected in any condition. However, in another study (Lapetite & Soulairac, 1951), thiouracile affected hoarding in rats, with results discrepant by sex: for males, thiouracile decreased hoarding, whereas for females, it increased hoarding.

Rat data on hoarding: Genetic evidence. There are marked differences in the hoarding performance of several strains of rats regardless of sex. For example, among three inbred strains of rats tested, black-hooded nonagouti rats had an earlier onset of hoarding, and larger pellet collection and hoarding persistence during satiation compared with the other two strains (brown-hooded agouti and Irish agouti) under experimental conditions (Stamm, 1954). The progeny of these groups (F1, offspring of the high-hoarding strain rats with low-hoarding strain rats, and Fb, backcrossed members of the F1 group to the low-hoarding parental strain) were later tested in a hoarding experiment, which revealed that hoarding scores from the F1 groups were similar to those of their high-hoarding parents, and that hoarding scores for the Fb group were widely and bimodally distributed. The author concluded that rat hoarding is due to a single dominant gene, although the contribution of multiple genetic factors was not tested (Stamm, 1956). One criticism of this study is that the design did not include an F2 or other backcross generation, preventing definitive conclusions about the hoarding gene's mode of transmission. However, these studies established the heritability of hoarding in rats, which later studies have found to be moderate to high (Manosevitz, 1965; Manosevitz & Lindzey, 1967), paralleling findings in humans (Wendland et al., 2009).

Evaluation of a Rat Model of Compulsive Hoarding Behavior in Humans

There are several reasons to believe that a rat model of human hoarding is promising. First, both species engage in larder hoarding that increases with age, without consistent sex differences. Second, rats and humans show the same dose-dependent response of hoarding behavior to amphetamine administration. Third, rats and humans with hoarding both evidence abnormalities in such brain areas as the NAcc and the mPFC. This finding supports the claim of Anderson et al. (2005) that normal hoarding behavior in humans and rats is organized subcortically, becoming disrupted only by impairment to such cortical areas as the mPFC, responsible for the regulation of hoarding. Consistent with this model is the idea that some hoarding behavior (perhaps more appropriately referred to as acquiring/storing behaviors) is normal for humans, and such behavior becomes pathogenic following cortical impairment. However, this hypothesis needs to reconcile the fact that "hoarding" refers to both normal and abnormal behaviors in rats but implies pathology in humans. Thus, distinguishing impaired hoarding from normal hoarding behavior in rats is critical to establishing a comparative basis to similar behaviors in humans. Fourth and finally, although the data are scant and older, genetic data on hoarding in rats suggest moderate to high heritabilities, apparently similar to those found in humans.

At the same time, a number of limitations with the literature raise questions concerning the rat model. The preponderance of neurobiological data on hoarding in rats dates back to the mid-20th century and has not been replicated using newer methodologies. Additionally, although researchers have stated that rats hoard food (and even inedible objects) in the wild (Lore & Flannelly, 1978; Wallace, 1994), few studies[3] have documented the effects of rats' hoarding in their natural habitat.

Primate Data on Hoarding

Although nonhuman primates are humans' closest genetic relatives, data substantiating hoarding behavior in primates are extremely limited. Only three species of primates, macaque monkeys (Stern & Passingham, 1994) and Barbados green monkeys (Baulu, Horrocks, & Rossi, 1980), have been explicitly linked to hoarding behaviors, and, to a lesser extent, squirrel monkeys (Marriot & Salzen, 1979). There is also an implication that chimpanzees store meat in one text (Jolly, 1972), but this behavior is not elaborated upon here or elsewhere. Because the literature for hoarding in primates is sparse, we include it here only because of the preference to find an animal species closer to humans for documenting parallels in hoarding behaviors.

Primate data on hoarding: Behavioral evidence. Monkeys, such as macaques, have cheek pouches in which they store food and, when food is limited, use for storing as much food as possible (Stern & Passingham, 1994). Some researchers have investigated the adaptive value of cheek pouch storage and determined that a predation-avoidance hypothesis best describes the data (L. W. Smith, Link, & Cords, 2008). However, because cheek pouch storage has not been explicitly associated with hoarding, any connection between the two behaviors is speculative.

In contrast, the Barbados green monkey has been observed hoarding apples, the first documented case of explicit hoarding behavior in nonhuman primates (Baulu et al., 1980; Vander Wall, 1990). The green monkeys of Barbados live in groups in densely forested areas but have been observed venturing into populated areas of the island during the morning or late afternoons to raid the fruit trees of inhabitants' yards. In this study, a dominant male of a group of 20 was the first to approach a yard, followed by the rest of the group, all of which proceeded to pick apples. One subadult male was observed to pick apples and place them in a cache, a hole between two rocks at the base of the tree; however, the apples were soon consumed after their placement in the cache (in other words, the storage period was extremely short term).

Finally, squirrel monkeys in one study (Marriot & Salzen, 1979), stored and aggressively defended food caches (and, interestingly enough, toys items as well) in plastic cup containers on the outside of their cages. Although Vander Wall (1990), classes this behavior as hoarding because of the storage, defense, and eventual retrieval of the items, a single study of these behaviors in squirrel monkeys is not enough to constitute compelling evidence for hoarding in the species as a whole, highlighting the need for further study.

Primate data on hoarding: Neurological evidence. In one study in which two groups of macaques (half of which received bilateral NAcc ibotenic acid lesions) were trained in two food search tasks (a four-box search task for group one and a 10-box search task for group two), lesions to the NAcc resulted in impaired, disorganized hoarding, such as less consistency in using right-to-left sequencing strategies in retrieving food from four storage boxes placed in a row or in lessened ability to organize behavior required to sequentially pick up the nut, peel the nut from the shell, discard the shell, and store the nut in the cheek pouch (Stern & Passingham, 1994). In another study, monkeys with damage to the DLPFC performed poorly at a similar food search task (Stephens et al., 2007).

Primate data on hoarding: Biochemical evidence. Although the biochemical correlates of hoarding or hoarding-like behaviors in nonhuman primates have not yet been studied, it will be important to investigate the role of glutamatergic and, especially, dopamine signals, given that (a) dopamine plays a key role in reward signals for primates (Schultz, Tremblay, & Hollerman, 2000), and (b) both neurotransmitters are implicated in human hoarding.

Primate data on hoarding: Genetic evidence. Candidate genes for hoarding in nonhuman primates have not yet been

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[3] In one of the few studies measuring hoarding in wild rodents, as opposed to laboratory-reared rodents, Zhang and Wang (2011) found significant differences in hoarding behaviors between the reared juvenile and both juvenile and adult wild rats, whereby reared juveniles hoarded less than either of the wild groups.

examined, most likely because the existence of hoarding in primates is a source of debate.

Evaluation of Primate Model of Hoarding in Humans

The fact that there are so few nonhuman primate models for hoarding in humans is problematic for the evaluation of this model. Another disadvantage of the primate model is that even in behavior that may arguably fall under the heading of hoarding behavior, such as cheek pouch storage in Old World Monkeys, one of the key features of hoarding for humans and other species—the remote storage of the hoarded object away from its source—is largely absent, with the exception of only one documented instance of storage in plastic cup containers in close proximity to the cages of squirrel monkeys in captivity (Marriott & Salzen, 1979).

Nonetheless, it is promising that, within the few hoarding studies that exist, the NAcc has been implicated, as it has for humans (and rats) who hoard. Furthermore, the behavioral suite of impulsivity, emotionality, disorganization, and hyperactivity accompanying impaired hoarding in lesioned monkeys bears some similarity to the cognitive impairments accompanying hoarding behavior in humans, particularly impulsivity and disorganization.

Overall, it is premature to draw conclusions concerning the fit of nonhuman primate models to human hoarding. Of all animal models, further investigation of nonhuman primate hoarding is most urgently needed given their taxonomic proximity to humans.

Analogous Hoarding in Animals and Humans?

In conclusion, significant evidence has accumulated to show that hoarding behavior has evolved several times across a wide variety of taxa (Källander & Smith, 1990; Smith & Reichman, 1984; Vander Wall, 1990), prompting a recent interest in animal models of compulsive hoarding in humans (An et al., 2009; Kellett, 2007; Preston et al., 2009; Tolin et al., 2009). Although animal models are never fully isomorphic with humans, many areas of psychopathology have been aided by their use and understanding. To both evaluate the validity of using an animal model for hoarding and to determine whether such a model would yield explanatory power for compulsive hoarding in humans above and beyond existing models (e.g., the cognitive–behavioral model), we compared data on human hoarding with hoarding behaviors in a variety of animal species. One of the first problems encountered in the current review was the sizable gap in each body of literature across species (e.g., lack of genetic evidence for hoarding among rats and birds; lack of sufficient construct validity for hoarding in primates). This dearth becomes more apparent when coupled with inadequate synthesis of the discrepant but related literatures. As a consequence, there is substantial variability in the strength of various animal models for hoarding in humans.

The rodent model of human hoarding appears to be the most compelling at present. Nevertheless, this model is characterized by a variety of strengths and weaknesses. In its favor, many areas of the brain implicated in compulsive hoarding in humans, such as the mPFC, have been associated with hoarding behavior in rats. There is at least some evidence that hoarding in rats is a primitive response integrated subcortically, and that increasing levels of hoarding are due to the release of subcortical structures from cortical inhibition (Zubek, 1951). This model is similar to Anderson and colleagues' (2005) model for hoarding in humans, whereby cortical insult releases subcortically driven hoarding. These hypotheses, along with neurological evidence, are consistent with a specific animal model—the rat model—for compulsive hoarding in humans.

One area that is problematic for the rodent model is the genetic differences between rats and humans. Furthermore, the dominance of experimental over naturalistic methods in rat hoarding data, and gaps in the literature for areas such as age and sex differences, are also problematic. For these reasons, rat models of humans remain promising but preliminary.

Avian models of human hoarding are intriguing but less convincing because of increased genetic dissimilarity to humans, behavioral differences such as scatter hoarding, minimal evidence for neurological overlap in hoarding in birds and humans, and virtually no biochemical or genetic data on avian hoarding. And although nonhuman primates are the most likely candidate for animal-based modeling of human hoarding, there is insufficient evidence to support such a relationship. Few studies have examined hoarding among primates, so it is debatable whether superficially similar behaviors, such as cheek pouch storage, can be considered as indicators of human hoarding. More research is needed to clarify the relationship between primates and hoarding-like behaviors and to identify neural, genetic, and biochemical correlates of primate hoarding to serve as a comparative basis for humans.

In summary, animal models of hoarding remain an important area for further investigation but vary widely in their validity for comparison with clinical hoarding in humans. Rodent models have shown the most promise as an animal model, largely because of similar neurology to humans implicated in hoarding behavior (An et al., 2009; Anderson et al., 2005; Grisham et al., 2007; Mataix-Cols, Rosario-Campos, & Leckman, 2005). However, the lack of a nonhuman primate model for hoarding, as well as the great diversity in hoarding behavior and type of species that hoard, render a robust analogy between hoarding in humans and animals provisional at present.

More extensive genetic research across species is especially needed across hoarding animals if the nature of the comparison with compulsive hoarding in humans is to be made more explicit. If more extensive data were to emerge supporting an animal model of compulsive hoarding in humans, they could be helpful in understanding the pathology of hoarding and in aiding its classification and treatment. The potential to go beyond the prevailing cognitive–behavioral model of hoarding is offered by an animal model because of the ability to model physiological processes that may underlie the behavior. Nevertheless, pending more compelling evidence to support an analogy between animal and human hoarding, the cognitive–behavioral model possesses the most explanatory power.

Only recently has attention begun to shift toward neurological, biochemical, and genetic influences on compulsive hoarding in humans. Future studies should collect not only more national but also more international epidemiological data to identify the conditions and variables associated with hoarding across differing cultures. Most of the variables for which animal hoarding behaviors have been tested—such as the effects of nutritional depletion, population density, seasonal variation, and sensitivity to temperature/photoperiod on hoarding—have not been tested in humans.

For example, in a recent field study of nonhibernating kangaroo rats, winter months were associated with larder hoarding, whereas summer months were associated with scatter hoarding (White & Geluso, 2012). This intraspecies variation in hoarding may be important to examine in humans, such as by determining if there are higher rates of hoarding among humans in colder, more northern territories. Although these factors may play less of a role in human hoarding because of their connection to food as the hoarded material, it is important to collect data on hoarding prevalence and the correlates of this prevalence across geographical regions.

If studies were to yield evidence of similarities in hoarding in humans and animals in these and other variables, such findings would provide some support for an evolutionary hypothesis of hoarding in humans. Nevertheless, this is a resounding "if," and the present data are far from being interpretable in an evolutionary context.

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Correction to Andrews, Lilienfeld, and Duke (2013)

In the article "Evaluating an Animal Model of Compulsive Hoarding in Humans" by Jenna G. Andrews, Scott O. Lilienfeld, and Marshall P. Duke (*Review of General Psychology*, Vol 17, No. 4, pp. 399–419. doi:10.1037/a0032261), the affiliation and name of author Jenna G. Andrews of Morehouse College were incorrectly listed in the byline and author note as Jennifer G. Andrews-McClymont of Stephens College. The online version of this article has been corrected.

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