Self-regulation and the *foraging* gene (*PRKG1*) in humans

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Foraging is a goal-directed behavior that balances the need to explore the environment for resources with the need to exploit those resources. In *Drosophila melanogaster*, distinct phenotypes have been observed in relation to the *foraging* gene (*for*), labeled the rover and sitter. Adult rovers explore their environs more extensively than do adult sitters. We explored whether this distinction would be conserved in humans. We made use of a distinction from regulatory mode theory between those who "get on with it," so-called locomotors, and those who prefer to ensure they "do the right thing," so-called assessors. In this logic, rovers and locomotors share similarities in goal pursuit, as do sitters and assessors. We showed that genetic variation in *PRKG1*, the human ortholog of *for*, is associated with preferential adoption of a specific regulatory mode. Next, participants performed a foraging task to see whether genetic differences associated with distinct regulatory modes would be associated with distinct goal pursuit patterns. Assessors tended to hug the boundary of the foraging environment, much like behaviors seen in *Drosophila* adult sitters. In a patchy foraging environment, assessors adopted more cautious search strategies maximizing exploitation. These results show that distinct patterns of goal pursuit are associated with particular genotypes of *PRKG1*, the human ortholog of *for*.

foraging gene | self-regulation | locomotion | assessment | *PRKG1*

Searching for and securing food, foraging, is a fundamental and ubiquitous goal in the animal kingdom, observed across many species (1–3). Indeed, the *foraging* gene (*for*) affects behavior in species as diverse as the fruit fly (*Drosophila melanogaster*), honey bees, and nematodes (3). Manipulations of *for* gene levels are sufficient to modify the foraging behavior of multiple species despite the many genes involved in generating the behavior (3–5). The *for* gene accomplishes its major effects on behavior by regulating downstream genes (6). *D. melanogaster*, the best studied of these species, exhibits phenotypes, labeled rovers and sitters, that differ in foraging behavior (3, 7–10). Adult rovers explore their environment widely with longer search paths than do adult sitters. In contrast, adult sitters "hug" the boundary of a foraging environment, even after 24 h of food deprivation that would normally prompt wider exploration (3, 11). These patterns of behavior reflect differences in the extent to which animals favor exploring vs. exploiting their environs (12). In other words, foraging balances the need for exploration [to avoid opportunity costs (12)] and exploitation of resources. Despite its ubiquity across species, how animals strike this balance between maximizing resource acquisition, while minimizing costs, is not well understood (13).

The search behaviors of adult rovers and sitters may be related, in part, to differing levels of risk aversion (3, 11, 14); that is, exploration carries with it some level of risk (15). In an empty arena, akin to rodent open-field tests (16), sitter flies move along the periphery hugging the edges, whereas rovers explore the center of the arena using what is known as darting exploration (14). These environs present the animal with a choice between sheltered and exposed regions (17). Thus, rovers could be said to show higher risk tolerance given their propensity to more fully explore their environs than sitters (3, 11, 14; a similar characterization in rodents is provided in ref. 18). In contrast, sitters manage risk by preferentially exploiting proximal resources (11).

Although research shows that the *for* gene's contributions to foraging varies within and between species (4, 5, 19–21), this balance between exploration and exploitation has not been investigated in humans. With respect to goal pursuit, humans display individual differences somewhat akin to rovers and sitters. Regulatory mode theory delineates self-regulatory modes of locomotion, which emphasizes execution of actions, a "just do it" approach, and assessment, which emphasizes evaluation of alternatives, a "do the right thing" approach (22). Individuals vary in the degree to which each mode is dominant in a given circumstance. What we suggest here is that those for whom locomotion is the dominant regulatory mode may behave in a conceptually similar manner to rovers; that is, they will explore their environment more extensively in the service of minimizing opportunity costs (23). In contrast, those with a dominant assessment regulatory mode may behave more like sitters, preferring to assess known quantities to choose the optimal way to exploit resources.

Foraging strategies observed in *D. melanogaster* can be attributed primarily to variation in a single gene, the so-called *for* gene (8–10). The human ortholog of *for*, known as *PRKG1*, also encodes a cGMP-dependent protein kinase (24). *PRKG1* proteins are found across the nervous system and are thought to underpin neuroplasticity and learning (25), and likely influence behavior in myriad ways. Variation in *PRKG1* was recently associated with interactions between maternal sensitivity and early life adversity (26) and between alcoholism and trauma (27).

Significance

We show that different genotypes of the human ortholog of the *foraging* gene, *PRKG1*, were associated with unique patterns of self-regulation. On a virtual foraging task, we show that these self-regulatory profiles also engaged distinct search strategies. One of the genotypes looks remarkably similar, in terms of foraging behavior, to a phenotype described in adult *Drosophila melanogaster*, the fruit fly. This phenotype, known as the sitter, tends to restrict exploration of the environment to local resources, a pattern we replicated in humans.

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However, its association with foraging and goal pursuit generally has yet to be examined. In two independent samples, we explored whether differences in the adoption of the distinct regulatory modes of locomotion and assessment would be associated with genotypes of rs13499, a single-nucleotide polymorphism (SNP) in the 3′ untranslated region (3′UTR) of *PRKG1*. In the first sample, we associated variations in rs13499 with self-reported preference for locomotion or assessment to determine whether the rover and sitter phenotypes are conserved in humans. Our second sample functioned as a replication with the addition of metrics obtained from two virtual foraging tasks to explore whether the different genotypes would be associated with characteristic goal pursuit patterns.

To investigate gene expression differences in rs13499 SNP variants, we accessed information from the CommonMind Consortium (CMC; https://www.synapse.org//#!Synapse:syn2759792/wiki/69613; 600 humans fully genotyped, including rs13499 SNP variants). In this sample, RNA expression levels from the dorsolateral prefrontal cortex (DLPFC) are measured for individual rs13499 variants. The DLPFC is critical for goal-directed behavior, executive control, and self-regulation (28, 29). The correlation computed between genotypes at rs13499 and DLPFC gene expression was significant at $P = 0.00232$ (30). The data showed higher expression in the C allele compared with the A allele.

Results

Sample 1. To assess the extent to which people adopt either a locomotion or assessment regulatory mode, we used an established self-report questionnaire (22). Predominance of regulatory mode was calculated as a difference score by subtracting assessment from locomotion scores: Positive scores indicate a predominant locomotion regulatory mode, and negative scores indicate a predominant assessment regulatory mode [regulatory mode predominance (RMP); *Methods*]. We used regression models to determine the influence of different genotypes on RMPs by coding the genotypes (AA = 0, CA = 1, CC = 2) and exploring the influence on RMP scores. Assessment predominance (Fig. 1) was highest for the homozygous AA genotype, a difference that approached significance ($F = 3.411$, $P = 0.067$ by the additive regression model; Fig. 1).

With respect to self-reported ethnicity, we examined differences in Caucasians (the largest ethnic group) and non-Caucasians (a combination of ethnicities) (*Methods*). The distribution of genotypes did not differ by ethnicity [$\chi^2(2) = 0.84$, $P = 0.66$], and no significant interactions were found between ethnicity and genotypes on all variables (all $P > 0.121$, t test). For sex, we found no differences across males and females on all measures (all $P > 0.483$) and no interaction between genotype and sex.

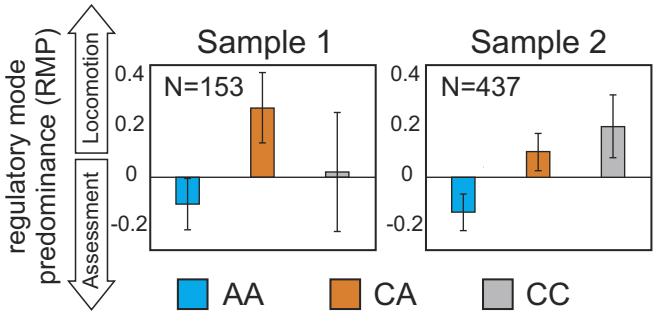

Fig. 1. RMP by genotype, in which the rs13499 polymorphism generates three genotypes (AA, CA, and CC). In sample 1, the genotype frequencies were 53% ($n = 81$), 34.4% ($n = 53$), and 12.6% ($n = 19$) for the AA, CA, and CC genotypes, respectively. In sample 2, the genotype frequencies were 45% ($n = 198$), 44% ($n = 192$), and 11% ($n = 47$) for the AA, CA, and CC genotypes, respectively.

Data from the sample 1 suggested that genetic variants in *PRKG1* (*rs13499*) differ in terms of preferred regulatory mode. Those with the AA genotype showed higher predominance for assessment, a more sitter-like phenotype, than those with the CA and CC genotypes. Interestingly, assessment is a more sitter-like phenotype, and the A allele has lower expression of PKRG1 in the DLPFC (CMC; https://www.synapse.org//#!Synapse:syn2759792/wiki/69613), analogous to the lower expression of *foraging* in sitter flies (9, 31).

Our selection criteria for this sample (*Methods*) led to a relatively small sample size for the CC genotype ($n = 19$). For sample 2, we tested a larger sample with balanced representation of sexes. In addition, participants performed two virtual foraging tasks (*Methods*) to explore differences in foraging search strategies that might correspond to phenotypes observed in sample 1.

Sample 2. Sample 1 results suggested an association between RMP and genetic variants in *PRKG1* (7, 11, 19, 26). Next, we aimed to replicate our findings in a larger sample while measuring search behaviors on an experimental analog of foraging. Participants performed two virtual foraging tasks in which they searched for "berries" on a touch screen in a limited time frame (*Methods*). Differences in goal pursuit, where they exist, should be evident in either individual metrics (e.g., path length, number of berries picked) or classification procedures demarcating search strategies (*Methods*). As with sample 1, we first explored the association between genetic variation and RMP. In sample 2, the rs13499 genotypes, AA (45%), CA (44%), and CC (11%), were in Hardy–Weinberg equilibrium [$\chi^2(1) = 0.01$, $P = 0.99$]. The distribution of genotypes did not differ across sex [$\chi^2(2) = 1.46$, $P = 0.48$]. As in sample 1, individuals with the homozygous AA genotype were associated with significantly higher assessment predominance (RMP) than those with the CA or CC genotype ($P = 0.007$, additive model). The difference was highly significant this time, with assessment predominance highest in the AA genotype (mean = −0.14, SD = 1.0), lowest in the CC genotype (mean = 0.2, SD = 0.86), and intermediate in the CA genotype (mean = 0.1, SD = 1.02) (note that negative numbers indicate an assessment preference; Fig. 1).

For sample 2, there were trends toward differences across males and females, although none reached significance. Nevertheless, males of the AA genotype had marginally greater assessment predominance (RMP; $P = 0.054$) and reduced locomotion scores ($P = 0.061$) compared with the CC genotype, with those of the CA genotype having intermediate scores. There was no significant association for assessment ($P = 0.704$). For females, those with the AA genotype had marginally greater assessment predominance compared with the CC genotype, with the CA genotype showing intermediate scores (RMD; $P = 0.069$). There was no significant association for locomotion ($P = 0.245$) or assessment ($P = 0.282$) scores (all statistics represent an additive regression model).

Next, we examined foraging performance as a function of genotype (Fig. 2 and Table 1). While there were trends evident across genotypes when examining individual metrics (Table 1), we ultimately chose to make use of classification analyses to comprehensively characterize search behavior. To do this, we first determined the distribution of recurrent spatial-temporal movement patterns used by each participant (32) (*Methods*). Individual search paths (*SI Appendix*, Figs. S1 and S2) were clustered into three categories based on movement profiles. Concordance between three clustering algorithms (*Methods*) was used to determine strategy cluster membership. A total of 76.2% of participants were characterized as either boundary-biased (59.4%) or systematic (16.7%) by all three clustering methods (Fig. 2*B*). The third group was classified as "mixed" (23.9%; Fig. 2*B*). Search paths within this group tended to meander or showed a combination of boundary bias and systematic strategies (*SI Appendix*, Fig. S1).

The three foraging strategies differed significantly in terms of path length ($P < 0.0001$, ANOVA). In contrast to the boundary-biased group, the systematic and mixed strategy groups had longer

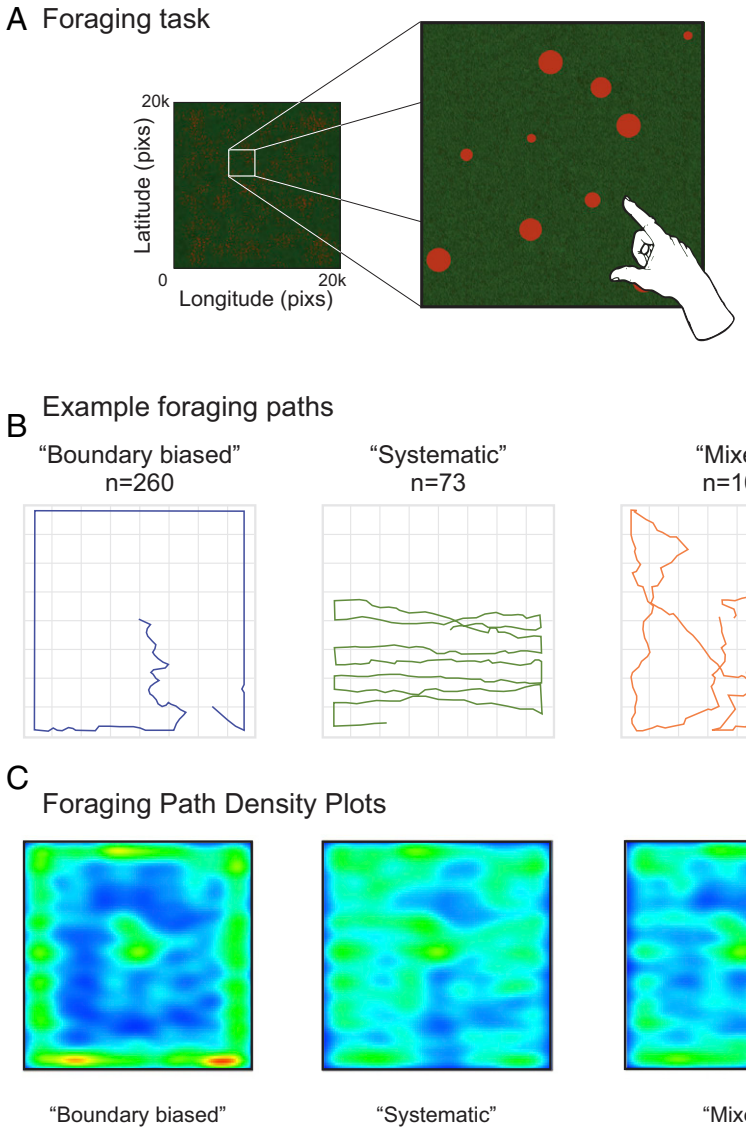

Fig. 2. (*A*) Schematic of the task environment. pixs, pixels. (*B*) Example search paths classified as boundary-biased, systematic, or mixed (*Methods*). (*C*) Density plots for all participants in each search strategy group.

path lengths [P adjusted < 0.00001, Tukey's honestly significant difference (HSD)]. The systematic and mixed groups did not differ on path length (P adjusted = 0.95, Tukey's HSD). The three groups differed in terms of average turning angle ($P < 0.00001$, ANOVA), with the systematic group having smaller average turning angles than either the boundary-biased or mixed group (P adjusted < 0.0001 and P adjusted < 0.0027, respectively, Tukey's HSD). The mixed strategy group had a smaller average turning angle than did the boundary group (P adjusted = 0.023, Tukey's HSD). There were no differences across groups in the number of berries picked ($P = 0.203$, ANOVA; Table 1).

Our assay of human foraging behavior suggests that humans cluster into three distinct search strategies, one of which, the boundary-biased group, resembles behavior observed in adult sitter *D. melanogaster*. The other two groups, although distinct from one another, tended to cover more of the search environment, much like the rover fly.

Those with the AA genotype were more likely to adopt a boundary-biased search strategy (compared with either the systematic or mixed group) than the CC genotype, with the CA genotype showing an intermediate preference for this strategy ($P = 0.02$, additive model). Thus, variation in rs13499 is associated with foraging strategy choice in a manner consistent with the adult sitter phenotype in the fly. In other words, those with the AA genotype of rs13499 demonstrate a stronger assessment orientation and tend to hug the boundary of the search environment in much the same manner observed in the *Drosophila* "sitter" phenotype.

The foraging task first used here had berries spread uniformly throughout. This does not represent typical environments faced by animals or humans in which resources are sparsely distributed, forcing exploration decisions. Therefore, we had the same participants forage in an environment in which berries were sparsely distributed (labeled "patchy"; *Methods*). In this instance, task metrics did differentiate between genotypes (Fig. 3 and Table 1). With respect to berry size, individuals with the AA genotype picked smaller berries than those with the CA genotype, who, in turn, picked smaller berries than those with the CC genotype ($P = 0.002$). Similarly, those with the AA genotype stopped to pick berries in patches with fewer berries visible. For this metric, those with the CC genotype had the highest scores, with those with the CA genotype having intermediate scores ($P = 0.003$; Fig. 3 and Table 1). This latter effect was marginally significant in the uniform environment (Table 1). There was no influence on the total number of berries picked ($P = 0.959$) or path length ($P = 0.707$) (all statistics represent an additive regression model; Table 1).

These results show that the AA genotype is associated with exploiting the local environment more extensively, picking

Table 1. Metrics from the foraging task (sample 2) for uniform and patchy berry distributions

	AA		CA		CC			
	n = 198 (51% male)		*n* = 192 (52% male)		*n* = 47 (43% male)			
Variable	Mean	SD	Mean	SD	Mean	SD	*F*	*P*
Uniform foraging environment								
Path length, pixels	139,267	24,836	139,547	22,178	139,213	24,207	0.00	0.963
No. of moves	249	49	249	55	248	47	0.03	0.885
No. of berries picked	152	20	154	21	150	23	0.00	0.959
Turning angle	33.56	10.53	35.31	11.1	32.99	10.45	0.29	0.591
Berry size, pixels	6.62	0.22	6.62	0.21	6.61	0.28	0.02	0.881
Berries visible	1.84	0.18	1.86	0.19	1.89	0.18	3.65	0.057
Patchy foraging environment								
Path length, pixels	143,769	25,967	147,084	25,593	142,259	27,362	0.14	0.707
No. of moves	263	55	257	56	254	57	1.65	0.199
No. of berries picked	147	25	153	22	149	27	2.65	0.105
Turning angle	34.19	10.24	34.44	10.31	33.37	9.75	0.42	0.838
Berry size, pixels	6.64	0.19	6.68	0.19	6.73	0.17	10.10	0.002
Berries visible	2.06	0.25	2.12	0.26	2.16	0.23	8.63	0.003

berries as they are encountered (as opposed to stopping to pick berries only when many are visible) and picking all available berries (even smaller, more difficult-to-"pick" berries). There was no relationship with the number of berries picked (P = 0.105), indicating that the AA genotype is associated with adoption of a more risk-averse strategy akin to sitters.

As for sample 1, we examined the influence of ethnicity by contrasting Caucasians (the largest ethnic group) and non-Caucasians (a combination of a range of ethnicities). The distribution of genotypes did not differ by ethnicity [$\chi^2(2) = 0.54$, $P = 0.76$], and no significant interactions were found between ethnic group and rs13499 genotypes on all study variables. There were some minor differences evident for individual metrics based on ethnicity. In contrast to non-Caucasians, Caucasians had higher locomotion scores ($P = 0.0215$, t test). Within the uniform environment, Caucasians more often adopted a systematic strategy ($P = 0.043$, t test), were less likely to adopt a boundary bias ($P = 0.056$, t test), made fewer movements ($P = 0.03$, t test), and picked more berries ($P = 0.04$, t test). Within the patchy environment, Caucasians exhibited smaller turning angles (P = 0.008, t test). There were no significant interactions between sex and rs13499 genotype on all foraging metrics.

Discussion

Our results show that genetic variation in *PRKG1* associates with distinct regulatory mode preferences and characteristic search patterns on our foraging task. In other words, in our assay of human foraging, we observed three distinct search strategies: boundary-biased, systematic, and mixed. The first of these, boundary-biased, was prominently associated with the AA genotype at the rs13499 SNP, a genotype that also tended to adopt an assessment regulatory mode. The latter association was evident in both samples, but more robustly in sample 2 (Fig. 1). The opposite claim, that those with the C allele resemble rovers, is more difficult to substantiate but warrants further research. Certainly, those with a C allele were less likely to hug the boundary of the environment than were those with the AA genotype. At the very least, the similarities observed here in two samples between sitters and assessors and their association with *PRKG1/for* across such phylogenetically distant species as humans and fruit flies imply an adaptive component to this profile.

We have cast the distinct profiles of the rover/sitter and locomotor/assessor in terms of risk tolerance. The more extensive foraging paths seen in rovers reflect a higher level of risk tolerance. Although not as relevant for humans, any exploratory behavior in animals carries some level of risk, including greater exposure to predators. The more extensive search paths of the rover indicate the animal is willing to accept those risks in the pursuit of resources. Similarly, the human locomotor can be thought of as showing higher risk tolerance, preferring to "get on" with things. The contrasting claims can be made for sitters/assessors. In the fruit fly, the sitter tends to explore its environs more cautiously, hugging the boundary of the environment, rather than risking forays further afield to more exposed regions (11, 19). Our strongest association here is with human assessors, who show behaviors that bear a remarkable resemblance to this phenotype in the fruit fly. They are more likely to adopt a boundary bias; to begin picking berries even when the visible cache of berries is small (or smaller relative to the stopping rule chosen by those with the C allele; Fig. 3 and Table 1); and to pick even the hard-to-get, smaller berries, perhaps not wanting to

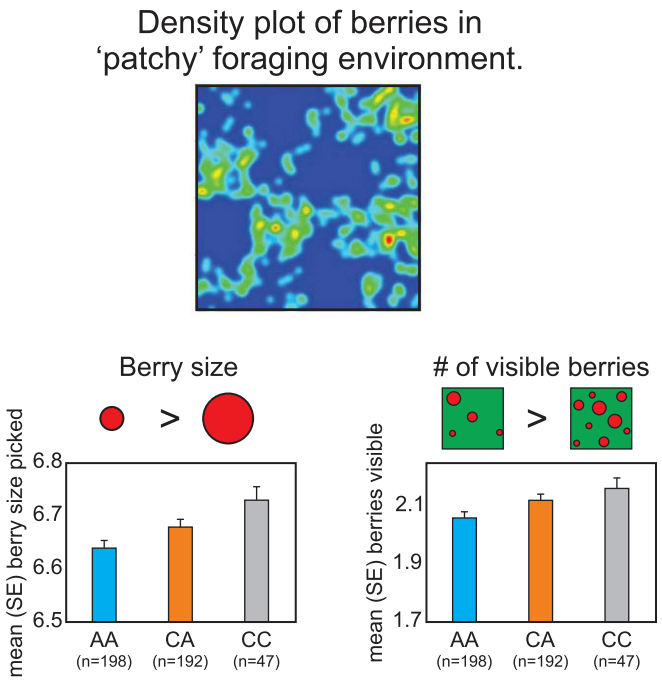

Fig. 3. (*Upper*) Density plot of berries in the patchy environment. (*Lower*) Differences in mean (±SE) size of berry picked (*Left*) and number of berries visible when stopping to pick (*Right*) by genotype (AA, blue; CA, orange; CC, gray).

waste any available resources. Although we are casting these differences in terms of risk tolerance, it is worth noting that we have not directly tested risk tolerance or aversion here. Future work could explicitly manipulate levels of risk [e.g., using tasks such as the Iowa Gambling Task (33)] to more directly examine the relation between risk aversion and self-regulatory profiles. Any variation in adopted regulatory mode in humans likely depends on many genes and their interactions, with one's preference for assessment or locomotion not solely driven by variation in *PRKG1*. Genes known to regulate dopamine, a neurotransmitter involved in calculating value and reward signals in the brain, represent another likely target, among many, for exploring the genetic contributions to self-regulation (34).

We used a composite measure of regulatory mode preference, one commonly used in the literature (35), to explore differences in behavior and genotype. It remains the case that one can adopt either regulatory mode as circumstances dictate (22). So how robust are such preferences across time? The original work on assessment and locomotion (22) showed cross-temporal stability responses were quite high (locomotion: $r = 0.77$, assessment: $r = 0.74$). In addition, across multiple large samples, we have shown robust associations between regulatory mode and other individual difference metrics [notably, boredom proneness, which is robustly negatively correlated with locomotion and positively correlated with assessment (36)]. With respect to foraging performance, more direct data are required. A comparison of performance across the two environs, although problematic given that each environment is explicitly expected to engender different behaviors, showed that 75.3% of participants who adopted a boundary bias in the uniform environment also did so in the patchy environment. Clearly, more research is needed to explore the consistency of behaviors across time in the same environments and across different tasks that rely on efficient self-regulatory control.

We showed an association between human regulatory mode preferences and foraging behavior akin to that observed in the adult fruit fly sitter. Using an assay of human foraging, we showed, perhaps unsurprisingly, that human foraging is more complex than the rover and sitter phenotypes well characterized in *D. melanogaster* (7, 9, 10). Humans show at least three distinct foraging strategies. How these strategies, along with variation in *PRKG1*, relate to other aspects of goal pursuit requires further work. In humans, genetic variation in *PRKG1* is related to maternal sensitivity to adverse events early in life (26), and is implicated in the relation between alcoholism and trauma (27). In addition, there are a multitude of associations between the *for* gene and behavior in the fruit fly that warrant investigation in humans, ranging from stress responses to learning and memory (19). The suggestion here is that the human ortholog of the *for* gene plays a key role in the regulation of behavior across many domains.

Methods

Sample 1 Information. Participants for sample 1 were recruited from a larger sample of 870 college students who completed a range of questionnaires, including the regulatory mode scales used here [a full description of the larger sample is provided by Shrout et al. (37)]. The sample used here (sample 1) represents a subsample of this group chosen to represent the extremes of regulatory mode dimensions. To do this, we chose participants whose locomotion or assessment scores fell in the upper or lower tertile of the larger sample to ensure that scores on these domains were high or low on at least one dimension. This gave us a sample of 575 participants from which we randomly drew 153 participants (117 females, mean age = 18.99 y, SD = 1.52) to collect genetic information. In terms of ethnicity, 55.6% identified as white/Caucasian, 26.5% as Asian, 8.6% as black, and 2.6% as biracial, with 6.6% responding "other" or declining to answer. It is worth noting that our sampling methods meant that the distribution of genotypes in sample 1 was unlikely to be representative of the larger sample from which they were drawn or, indeed, the general population, problems we rectified in sample 2. Written informed consent was obtained from each participant before commencing the study, which was approved by the Columbia University Institutional Review Board in 2011 and was conducted between September 2011 and March 2012.

Sample 2 Information. For sample 2, a total of 450 undergraduates from the University of Waterloo participated. Data were collected during the Fall 2015, Winter 2016, and Winter 2017 academic terms. All participants completed the regulatory mode questionnaires and two variants of the foraging task, as well as providing a saliva sample. Of the 450 participants, data for 13 were incomplete and excluded from further analysis (final sample = 437, 215 females, mean age = 19.99 y, SD = 2.62; one participant did not disclose his/her sex). A total of 43% identified as white/Caucasian, 25% as East Asian, 14% as South Asian, 3.9% as Southeast Asian, 3.7% as Middle Eastern, and 3.4% as black/African, and 9.5% identified with other ethnic groups. A total of 2% declined to indicate their ethnicity. Written informed consent was obtained from each participant before commencing the study, which was approved by the Office of Research Ethics at the University of Waterloo in February 2015.

Genotype, Ethnicity, and Sex. We contrasted the two samples in terms of ethnicity with the samples split by Caucasian and non-Caucasian. The two samples differed in terms of ethnicity [sample 1: Caucasian = 84, non-Caucasian = 67; sample 2: Caucasian = 187, non-Caucasian = 250; $\chi^2(1) = 6.936$, $P < 0.008$]. This likely reflects a number of things, including the distinct communities from which the samples were drawn and the selection criteria applied to sample 1. The distribution of genotypes was independent of ethnicity [$\chi^2(2) = 0.478$, $P = 0.79$; sample 1, genotype proportions for Caucasian: AA = 0.5, CA = 0.36, CC = 0.14; genotype proportions for non-Caucasian: AA = 0.57, CA = 0.33, CC = 0.10; sample 2, genotype proportions for Caucasian: AA = 0.44, CA = 0.44, CC = 0.12; genotype proportions for non-Caucasian: AA = 0.46, CA = 0.45, CC = 0.09].

Sample 1 did not have equivalent representation of males and females. Therefore, we did not examine differences in genotype distribution based on sex for this sample. For sample 2, genotype distribution was independent of sex [$\chi^2(2) = 1.47$, $P = 0.481$; for males: AA = 0.45, CA = 0.42, CC = 0.13; for females: AA = 0.46, CA = 0.45, CC = 0.09]. The distribution of genotypes was in Hardy–Weinberg equilibrium for both sexes (males: $\chi^2 = 0.456$, $P = 0.499$; females: $\chi^2 = 0.607$, $P = 0.436$).

DNA Collection, Extraction, Polymorphism Determination, and Gene Expression. DNA collection, extraction, and polymorphism determination procedures were identical for both samples. The Oragene OG-500 DNA Kit (DNA Genotek) was used for DNA collection from saliva samples (~2 mL). DNA extraction was done according to the manufacturer's instructions. The Clinical Genomics Centre in Toronto performed the DNA isolation, quantitation, normalization, and SNP genotyping on the saliva samples.

The *PRKG1* gene is located on chromosome 10, cytological location 10q11.23-21.1, with a molecular location between 50,991,358 and 52,298,350 bp. Selected SNPs within the *PRKG1* gene occurred in protein coding regions (exons) or the 3′UTR and were predicted to either affect protein function or influence the regulation of *PRKG1* mRNA transcripts. The SNPs in the exonic regions of *PRKG1* were monomorphic in our sample and are not discussed further. The rs13499 SNP lies in the 3′UTR of *PRKG1* that is adjacent to the kinase domain, common to all transcripts. The variant rs13499 is located at chr10:52297965 (GRCh38.p7), mapping to the 3′UTR of *PRKG1* and the intronic region of *PRKG1-AS1*, a long noncoding RNA that is likely coexpressed with *PRKG1*. The genomic location of rs13499 resides in four different *PRKG1* mRNA transcripts, suggesting a gene regulatory role for this SNP. This SNP (rs13499) showed significant variation across individuals. This SNP had a minor allele frequency (MAF) in our sample 1 of C = 0.301 and in sample 2 of C = 0.335, which is similar to the global MAF of C = 0.3111/1,558 (1,000 genomes). The rs13499 polymorphism generates three genotypes: AA, CA, and CC. In sample 1, the genotype frequencies were 53% ($n = 81$), 34.4% ($n = 53$), and 12.6% ($n = 19$), while in sample 2, the frequencies were 45% ($n = 198$), 44% ($n = 192$), and 11% ($n = 47$) for the AA, CA, and CC genotypes, respectively.

SNP genotyping for each sample was done as part of larger studies. Details of identical methods used can be found in a study by Sokolowski et al. (26). Briefly, samples were genotyped using MALDI-TOF mass spectrometry via the MassARRAY System (Agena Bioscience). This approach uses multiplexing to assay multiple SNPs for each sample simultaneously and entails the single-base extension of an oligo probe designed to anneal directly adjacent to an SNP of interest. Data were analyzed using MassARRAY Typer software (v 3.4). Each multiplex reaction was assessed using standard quality control parameters and poorly performing SNPs, and/or samples were disqualified.

Regulatory Mode Questionnaire. The regulatory mode questionnaire measures individual differences in locomotion and assessment regulatory modes (22). Each regulatory mode orientation is assessed by a 12-item subscale (e.g., "By the time I accomplish a task, I already have the next one in mind";

endorsing this item indicates a locomotion preference) rated on a six-point Likert scale ranging from "strongly disagree" to "strongly agree." High scores reflect greater emphasis of either the locomotion or assessment mode. Kruglanski et al. (22) reported an internal consistency of 0.82 for the locomotion scale and 0.78 for the assessment scale, and test-retest reliability of 0.77 for the locomotion scale and 0.73 for the assessment scale.

The RMP score was calculated by subtracting assessment from locomotion scores and scaling the difference score such that positive scores indicate a locomotion predominance and negative scores indicate an assessment predominance, a common approach to capturing the RMP within individuals (35).

Foraging Task. We developed an assay of human foraging programmed using Python 2.7 with the aid of PyGame (38). The task was shown on a touch screen placed flat on the table and inclined by ∼25° for ease of use (i.e., a vertical monitor would place undue strain on the shoulders). The foraging task consisted of a virtual 2D environment populated by red berries. The background was a grass-like texture (512 × 512 pixels) tessellated within a 20,000 × 20,000-pixel environment. The screen displayed only a portion of the environment at a time, encompassing 1,264 × 1,080 pixels. Participants navigated using their index finger to swipe the screen. Berries were red circles varying in size from a radius of four to 16 pixels. Three hundred eighty-four berries were present in the environment.

Two distributions of berries were used, labeled uniform and patchy. The uniform environment was segmented into 16 equal zones (5,000 × 5,000 pixels each), with each zone containing 24 berries (two of each size) pseudorandomly distributed such that no two berries could be 100 pixels from the center of another berry. The patchy environment consisted of four distinct zones (high-, medium-, and low-density zones and an empty zone). There were four zones of each type. High-density zones had 48 berries (four of each size), medium-density zones had 24 berries (two of each size), and low-density zones had 12 berries (one of each size). Zones were distributed such that no two zones of the same type were adjacent to each other (a density plot of berry distribution is given in Fig. 3).

In both environs, participants had to collect as many berries as possible within 5 min. The two environs were presented in counterbalanced order. A counter showing how many berries had been collected and a clock counting down the remaining time were displayed in the upper right corner. The task has a game-like feel to it and, as such, prior gaming experience may have influenced strategy choice. Exploring the influence of gaming experience and distinct priors on foraging represents a fruitful avenue for further research.

Foraging Classification Method. To identify search strategies used, we first determined recurrent movement patterns using recurrence-quantification analysis (RQA) (32). Search paths were first clustered using three separate algorithms, followed by human observer classification (*SI Appendix, Classification of Foraging Search Strategies*). Concordance across all methods was 76.5% for the algorithms and 75% for three human observers (example paths are shown in *SI Appendix*, Fig. S1).

Importantly, RQA analysis, the initial technique used to determine recurrent movement patterns (32), clearly showed differences in movement patterns that corresponded to the three groups derived algorithmically (*SI Appendix*, Fig. S2).

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