Individuals with ventromedial frontal damage have more unstable but still fundamentally transitive preferences

Classification:
Biological Sciences – Neuroscience
Social Sciences – Economic Sciences

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Abstract

Though the ventromedial frontal lobes (VMF) are clearly important for decision-making, the precise causal role of the VMF in the decision process has still not yet fully been established. Previous studies have suggested that individuals with VMF damage violate a hallmark axiom of rational decisions by having intransitive preferences (i.e., preferring A to B, B to C, but C to A), as these individuals are more likely to make cyclical choices (i.e., choosing C over A after previously choosing A over B and B over C). However, these prior studies cannot properly distinguish between two possibilities regarding effects of VMF damage: are individuals with VMF damage prone to choosing irrationally, or are their preferences simply more variable? We had individuals with focal VMF damage, individuals with other frontal damage, and healthy controls make repeated choices across three categories – artwork, chocolate bar brands, and gambles. Using sophisticated tests of transitivity, we find that, without exception, individuals with VMF damage made rational decisions consistent with transitive preferences, even though they more frequently exhibit choice cycles due to a greater variability in their preferences across time. That is, the VMF is necessary for having strong and reliable preferences across time and context, but not for being a rational decision maker. We conclude that VMF damage affects the noisiness with which value is assessed, but not the consistency with which value is sought.

Keywords: transitivity, lesion, ventromedial prefrontal cortex, decision-making

Significance statement

The VMF is a part of the brain that is thought to be one of the most important for preference-based choice. Despite this, whether it is needed to make rational choices at all is unknown. Previous studies have not discriminated between different possibilities regarding the critical necessary role that the VMF plays in value-based choice. Our study shows that individuals with VMF damage still make rational decisions consistent with what they prefer, but their choices are more variable and less reliable. That is, the VMF is important for the noisiness with which value is assessed, but not the consistency with which value is sought. This result has widespread implications for rethinking the role of VMF in decision-making.

Introduction

A central assumption of rational choice theories is that decision-makers compare the subjective value of different options and choose the highest valued option. Satisfying this assumption is equivalent to the observed choices being transitive (1). An example of transitivity is the following: If you choose to listen to Adele (A) over Beyoncé (B), and Beyoncé over Celine Dion (C), then you would also choose Adele (A) over Celine (C). There is a strong argument that choices ought to be transitive, as an intransitive chooser would consistently get caught in choice cycles that do not advance towards any goal (choosing A over B, B over C, and C over A), and could be exploited for this (e.g., an unsavory ticket hawker can keep charging you to trade for tickets to your ever-shifting more preferred artist). Thus, nearly all normative theories of decision-making are transitive.

Given this, one might expect that organisms develop internal representations of subjective value to ensure transitivity. Indeed, dozens of functional neuroimaging studies in humans and neurophysiological studies in non-human animals have now identified neural activity in the ventromedial frontal lobe (VMF) that scales with subjective value across different categories of goods (2-5). Correspondingly, lesions to the VMF impair value-based decision making in a variety of ways (6-10).

Identifying the precise role of the VMF in transitive preference and rational choice, then, is central to understanding the neural mechanism behind how we make choices that allows us to survive and thrive. Intriguingly, several previous studies have shown that individuals with

VMF damage make more cyclical choices (i.e., choosing C over A after previously selecting A over B and B over C) than healthy controls or individuals with damage elsewhere in the frontal lobe (11-13). However, this increase in cyclical choices after VMF damage is consistent with two very different possibilities regarding the necessary role of VMF, and putative value signals in VMF, in value maximization.

The first possibility is the choices of individuals with VMF damage are fundamentally intransitive and do not reflect a self-consistent set of underlying preferences. In the example above, the individual with VMF damage would consistently and reliably choose C over A. This could occur if individuals with VMF damage chose according to stimulus-response associations or rules that lack any higher order transitive structure, rather than any set of underlying preferences. If this possibility were true, the proper conclusion would be that an intact VMF is necessary for the human brain to assess value at all, or to use value to make decisions; that an intact VMF is necessary for transitive preferences and rational choice.

The second possibility is that the choices of individuals with VMF damage reflect preferences that are more variable. In this case, in the example above, the individual with VMF damage might prefer A over C on average, but less decisively than others. Thus, if asked again later, this individual would have a greater chance of changing their mind and now choosing C over A. This could occur if individuals with VMF damage chose according to underlying values, but the assessment of those values was noisier across time and context. If this possibility were true, the proper conclusion would be that an intact VMF promotes the stability and reduces the variability of valuations across time and context; but an intact VMF is not necessary for transitive preferences and rational choice.

Distinguishing between variable versus fundamentally intransitive preferences is a deep problem in testing theories of rational choice that has only somewhat recently been solved (14). Here we use these recently developed tests of a stochastic model of transitivity to determine whether the preferences of individuals with VMF damage are more variable or fundamentally intransitive. Importantly, these tests recognize that behavior in experiments is probabilistic, and therefore testing axioms of rational choice like transitivity requires recasting these axioms in probabilistic terms (14-17). Critically, from a probabilisitic perspective, noting a choice cycle (e.g., choosing C over A when one has chosen A over B and B over C), as done in previous studies, is not sufficient to disentangle whether one has fundamentally intransitive versus variable preferences. In contrast, if the choices of individuals with VMF damage do no satisfy tests of a stochastic model of transitivity, this would show that their preferences are fundamentally intransitive; while if their choices do satisfy such tests, this would suggest that their preferences are simply more variable. A definitive answer to this question will identify more precisely the necessary role of VMF, and putative value signals in VMF, in value-based decision-making.

Results

Choice Cycle

Individuals with frontal damage exhibit more choice cycles. A subset of the choices in our experiment, Set A, consists of a single instance of all pairwise choices from a total of nine or ten items within a category, which allows us to replicate two previous studies that documented a greater number of choice cycles in individuals with VMF damage (11, 12). Exhibiting cyclical choices is a necessary but not sufficient condition for violating stochastic models of transitivity. Combining all three reward categories (art, brands, gambles) in our experiment (Figure 2), we replicate the finding that individuals with VMF damage have more choice cycles than healthy controls (HC). Because three previous studies have found increased choice cycles after VMF damage (11-13), we conducted planned comparisons between groups. Similar to previous studies, our VMF group (mean = 9.93%, sd =6.65) made more cyclical choices than the HC group (mean = 5.71%, sd = 4.05; Wilcoxon ranked sums Z = 1.64, $p = 0.05$).

However, we do not replicate that this increase in cyclical choices is selective to VMF damage in the frontal lobe. Unlike previous studies, our frontal control (FC) group (mean = 9.09%, sd = 3.74) also made more cyclical choices than the HC group (Z = 2.05, $p = 0.02$) and the difference between VMF and FC and was not significant (Z = 0.12, $p = 0.45$). This increase in cyclical choices in the FC group, though, appears to be driven primarily by choices in the gamble category, a type of choice that has not been used in previous studies (see Supplementary Analyses; Fig. S1)

Differences among individuals. As the test of stochastic transitivity is performed at the level of individuals, we also examined the number of cyclical choices at the individual level. To do this, we considered each individual with a VMF or FC lesion as a single case, and compared their total number of choice cycles (i.e., across all three categories) against healthy controls. We made this comparison using case-control *t*-tests (18) which are modified to compare an individual against a normative group when the sample size is small. In the VMF group, four individuals made significantly more cyclical choices than healthy controls, before corrections for multiple comparisons (Subject 350: t(19) = 2.04, $p = 0.03$; Subject 10403: t(19) = 3.28, $p = 0.002$, Subject 12402: t(19) = 3.13, $p = 0.003$; Subject 775: t(19) = 3.13, $p = 0.003$). These differences remained significant in the latter three individuals after correcting for multiple comparisons using FDR (corrected $p = 0.023$ for all three individuals). Lesion extent of these three subjects is shown in **Figure 2b.** In contrast, in the FC group, none of the individuals made significantly more cyclical choices than healthy controls (all $p >= 0.05$ before multiple comparison correction).

This result suggests that a subset of individuals with VMF damage show the most pronounced increase in choice cycles. However, we did not find evidence to support any particular account of this heterogeneity. The total number of choice cycles (i.e., across all three categories) was not significantly correlated with lesion size (in cc's), whether considering all subjects with lesions (Spearman's rho = -0.14, $p = 0.51$) or only those with VMF damage (rho = -0.13, $p = 0.67$). Within the VMF group, the total number of choice cycles was also not significantly correlated with lesion volume within a vmPFC mask defined based on value effects in fMRI studies (2) (rho = -0.06, $p = 0.83$). Finally, across all subjects, the total number of choice cycles was not significantly correlated with any demographic variables (gender, point biserial r = 0.13, $p = 0.39$; age, rho = 0.14, $p = 0.35$; education, rho = 0.24, $p = 0.11$).

Tests of a Stochastic Model of Transitivity

Individuals with VMF damage make choices consistent with stochastic models of transitivity. We replicated previous findings that individuals with VMF damage make an increased number of cyclical choices. However, this observation alone is not sufficient to determine if the choices of these individuals are fundamentally intransitive versus more variable. Therefore, we next turned to the central question motivating our study, which is whether or not the choices of these individuals violate transitivity. To do this, we examined the subset of choices in our experiment, Set B, which involve 15 repetitions each of 10 different binary choices in each of the three categories. These data provide sufficient power for evaluating whether the choices each participant made are consistent with a stochastic model of transitive choice called the mixture model. The mixture model assumes that every choice is made according to a preference ordering, but that the preference ordering used for a given choice is drawn from a random mixture of possible orderings across all choices. As documented in the Methods below, and perhaps unintuitively, this model imposes rather restrictive constraints on the choice probabilities across the 10 binary choices in each category.

The results were unambiguous: across nearly all individuals tested, including those with VMF damage, choices were consistent with stochastic transitivity (127 of 129 total tests across all individuals and domains, **Table 2**). None of the individuals with VMF damage, including the three individuals who exhibited the largest number of choice cycles, violated the mixture model in any of the three domains (a total of 39 tests, **Table 2**). Similarly, none of the individuals with frontal damage outside the VMF violated the mixture model in any of the three domains (a total of 30 tests, **Table 2**). Only two healthy controls significantly violated the mixture model, and only in the gambles domain (p = 0.002 and p = 0.01, respectively, **Table 2**). Interestingly, both of these individuals followed Tversky (15)'s lexicographic semiorder heuristic, and so their results demonstrate the sensitivity of our test to detect individuals using attribute-based heuristics that lack higher order transitive structure.

Individuals with VMF damage are not choosing randomly. One possible explanation for why individuals with VMF damage conform to probabilistic models of transitivity despite making a greater number of cyclical choices is that they are simply choosing randomly, as completely random choices fulfill the random mixture model 80% of the time in our experimental design (see Supplementary methods). However, individuals with VMF damage are not simply choosing randomly. First, the probability that a group of random choosers the size of the VMF group (N=13) would all make choices consistent with the random mixture model in all three domains is extremely low, $p = 1.66e\text{-}04$. Second, we can directly evaluate the likelihood that an individual is choosing randomly by comparing their choice proportions (N=10 in each category) against a choice probability of 0.5. For every single individual with VMF damage, and in all three domains, the likelihood that their choice proportions arose from completely random choice was extremely low (all $p < 1e\text{-}06$).

Individuals with VMF damage do not have systematically different preferences. A second possible explanation for why individuals with VMF damage conform to probabilistic models of transitivity despite making a greater number of cyclical choices is that they have systematically different preferences. For example, we might expect that a risk-neutral chooser would be more likely to make occasional cyclical choices in our gambles category than a strongly risk averse chooser. However, individuals in the VMF group did not make systematically different types of choices than individuals in the other groups. In a MANOVA on the choice proportions for each of the 10 binary choices the participants faced in each category, there were no significant differences between groups in the art category [Wilks' Lambda = 0.64, F(18,64) = 0.9, *p* = 0.58], the brand category [Wilks = 0.64, F(18,64)=0.90, *p* = 0.58], or the gambles category [Wilks = 0.46, F(18,64) = 1.67, *p* = 0.07].

Individuals with VMF damage have more variable preferences. A third possible explanation for why individuals with VMF damage conform to probabilistic models of transitivity despite making a greater number of cyclical choices is that they have more variable preferences. That is, their choices reflect underlying transitive preference orderings, but they vacillate among preference orderings more than other choosers. To further test this possibility, we fit each individual's choices and response times (RTs) in Set B to a drift diffusion model (DDM) (19). This model assumed that choices and RTs were a probabilistic function of the rank distance between the two options in the average preference ordering for that individual (see Methods for details on how the average preference ordering was determined). Specifically, we modelled the decision process as a decision variable (DV) that increased linearly with a slope $d*v^{\alpha}$, where *d* was the drift rate, *v* was the rank difference between the two items, and α was an exponent accounting for potential non-linearities in the effect of rank difference. We also assumed that at each time step there is Gaussian noise added to the DV, with a standard deviation of ε, that there is a non-decision time (*ndt*) before accumulation begins, and that the DV takes an initial value (*int*) that is constant across trials. Fits to this model revealed that individuals with VMF damage were more variable choosers. The only parameter of the DDM that was significantly different across groups was the noise parameter ε [F(2,37) = 6.25, *p* = 0.005]. Specifically, the VMF group (mean = 0.12, sd = 0.03) had significantly higher ε than HC (mean = 0.09, sd = 0.04)[t(28) = 2.08, *p* = 0.047] and FC (mean = 0.07, sd = 0.02) [t(20) = 3.94, p < 0.001]. No other parameters differed between the three groups [drift rate, *d*: F(2,37) = 1.78, *p* = 0.18; non-linearity, α: F(2,37) = 0.06, *p* = 0.64; initial value, *int*: F(2,37) = 0.24, *p* = 0.79; non-decision time, *ndt*: F(2,37) = 0.02, *p* = 0.94; **Figure 3a].** This pattern was consistent across all three choice categories in the experiment (Fig. S2).

An examination of the RTs further supports the claim that individuals with VMF damage differ from healthy controls specifically in the noise parameter in the DDM (**Figure 3b**). An increase in the noise parameter causes faster RTs both on trials consistent with the average rank distance (“correct”) and those inconsistent with the average rank distance (“error”), while an increase in the drift rate, for example, would only cause changes in the former RT distribution. Compared to HCs, VMF subjects have a greater proportion of faster RTs for both “correct” and “error” trials. This pattern was also consistent across all three choice categories in the experiment (Fig. S3).

Discussion

Past demonstrations that individuals with VMF damage more frequently make cyclical choices (i.e., selecting C over A after previously selecting A over B and B over C; (11-13) cannot distinguish between two possibilities, with drastically different implications for the function of the VMF. One possibility is that individuals with VMF damage are fundamentally intransitive:

that they reliably choose in an intransitive manner when given the same choice between the same options repeatedly. A second possibility is that individuals with VMF damage are more variable in their choices, yet still fundamentally transitive. Here we provide a clear test between these two possibilities by evaluating whether the choices of individuals with VMF damage satisfy stochastic models of transitivity, as variable choosers would pass such tests but fundamentally intransitive choosers would not. We find overwhelming evidence that individuals with VMF damage are more variable but not fundamentally intransitive, as all individuals with VMF damage make choices in all domains that are consistent with stochastic models of transitivity.

We found definitive evidence that individuals with VMF damage are fundamentally transitive, that their choices satisfy stochastic models of transitivity. Not a single one of the VMF damaged patients violated stochastic transitivity, even as their decisions are more likely to exhibit choice cycles. Furthermore, we showed that this pattern was not due to individuals with VMF damage choosing in an entirely randomly manner, nor was it due to these individuals having preferences that were systematically different from those of the other groups. Rather, this pattern was due to individuals with VMF damage being more variable choosers. This is consistent with the suggestion of Henri-Bhargava, Simioni and Fellows (12) that “values are unstable, fluctuating from trial to trial in those with VMF damage.” We illustrated this by fitting a drift diffusion model (19) to each individual’s choices. In this model, the VMF group had a significantly higher noise term, i.e., more variance around the decision variable, than healthy individuals or those with frontal damage outside the VMF. Importantly, the VMF group did not differ from others in any other parameter of the DDM. Our modeling results further strengthen the conclusion that the VMF serves to make preferences more stable, so that individuals would be less likely to select an option that is typically less preferred.

These results are difficult to reconcile with the view that VMF is the only critical substrate for value-based choice. This view would predict that individuals with VMF damage would only be able to choose in a non-value-based manner, for example, according to rules or heuristics, and therefore be more likely to violate transitivity. In contrast, these results are easier to reconcile with a framework in which valuation and value-based choice are distributed processes, to which multiple regions of the brain contribute in some respect (20). This framework would predict that others regions can compensate for damage to the VMF, so that VMF damage does not fundamentally abolish the transitivity of preferences. As making transitive choices that maximize value is incredibly important to the survival of an organism, it would make sense that value is a highly conserved process that is not abolished by damage to one part of the cortex. Future studies could more directly test hypotheses about compensation by examining activity in inconsistent individuals with fMRI, as it is also possible that regions that compensate are in the still intact parts of VMF rather than in other regions entirely.

Future studies can further investigate how exactly the VMF supports the stability and reduces the variability of preferences. One possibility is that VMF contributes some part of the composition of subjective value. If subjective value is computed through the interaction of several brain regions, the loss of VMF may make this computation noisier and less reliable. An alternative possibility, though, is that the VMF contributes to the same preference ordering being repeated reliably, without contributing to valuation *per se*. For example, individuals might use episodic memories of their previous choices (e.g., “I remember choosing A over B before”) to guide their decisions, or a representation of the context of the experiment may activate a specific set of preferences, as in a schematic network. Previous work has shown VMF involvement in both episodic memory processes (21) and schema formation (22, 23).

Finally, we extended previous studies that considered the number of choice cycles by identifying heterogeneity in these effects both across individuals and across domains. There was considerable heterogeneity within the VMF group, where some participants made as few cyclical choices as healthy controls, while other participants made significantly more cyclical choices. We did not find any systematic differences in lesion location or size that accounted for this heterogeneity. The lesions of the three individuals in the VMF group who made significantly more cyclical choices overall did not overlap much in their location, and the overlap areas were in the same location where other individuals had sustained lesions. The lesions of these three individuals did tend to extend more posteriorly towards the basal forebrain and ventral striatum, though given the sample size in our study this potential explanation will need to be rigorously evaluated in future work with a larger number of subjects. Future studies could also test potential explanations that we were unable to assess by using more advanced imaging to test whether damage to specific white matter tracts or disruptions in specific connectivity networks are linked to making more cyclical choices.

In conclusion, we provide a clear-cut test of whether VMF is necessary for transitive preference and rational choice, and found that individuals with VMF damage make choices that are more variable, but were, without exception, fundamentally transitive. This result both characterizes how erratic choices manifest after damage to the VMF (24, 25), as well as potentially explains why studies using similar decision-making paradigms in individuals with

VMF damage can yield different results (26). Our findings further clarify and define the necessary role the VMF plays in value-based decision-making. Specifically, though each choice still reflects some subjective preference ordering after VMF damage, an intact VMF is necessary for these preference orderings to remain stable and reliable across time and contexts.

Methods

Experimental Design

Participants. Fourteen individuals with focal damage to the frontal lobes were recruited from the Focal Lesion Database (FoLD) at the University of Pennsylvania, and ten were recruited from the Cognitive Neuroscience Research Registry at McGill University (27). Individuals were eligible to participate if they had a lesion primarily affecting the frontal lobes. One individual was excluded due to incomplete data collection (the individual completed one session and was not able to be scheduled for the second). Fourteen females and 9 males were included in the final sample. Participants were tested a minimum of 5 months after injury (median = 10.29 years, range: 5 months to 17.75 years).

Participants were divided into two groups *a priori* based on location of damage, assessed with MR or computed tomography images by a neurologist blind to task performance. The ventromedial frontal lobe (VMF) group consisted of individuals who sustained damage to the VMF, while the frontal control group (FC) consisted of individuals who sustained damage to the frontal lobe sparing the VMF. Lesions were drawn on a common space [Montreal Neurological Institute (MNI) brain] by neurologists at the research sites blind to task performance. The overlap images for the groups are found in **Figure 1**. Damage in the VMF group was caused by aneurysm or subarachnoid hemorrhage in 5 cases, stroke in 2 cases, tumor resection in 3 cases, glioma in one case, and meningioma in 2 cases. Damage in the FC group was caused by hemorrhage, stroke or infarct in 7 cases, glioma in 2 cases, and meningioma in one case.

Age and education matched healthy controls (HC) were recruited from the corresponding Normal Control Databases of the University of Pennsylvania (N = 14) and McGill University (N = 6), including 15 females and 5 males (**Table 1**). They were free of neurological and psychiatric disorders. All subjects provided informed consent and were compensated for their time. The study protocol was approved by the institutional review boards of both the University of Pennsylvania and McGill University.

Apparatus. All tasks were programmed using EPrime 2.0 (Psychology Software Tools). Participants were tested at the Hospital of the University of Pennsylvania, at the MNI, or at their own home in the greater Philadelphia or Montreal area. Participants saw stimuli on a laptop monitor and responded using the 1 and 0 keys of the keyboard.

Stimuli. Stimuli consisted of images of artwork, chocolate bars, and pie charts representing gambles. There were two sets of stimuli: 10-11 stimuli for each of the categories (10 for chocolate bar brands, 11 for art and gambles) used in non-repeated choices that allow testing for choice cycles (set A), and 5 stimuli for each of the categories (art, chocolate bar brands, gambles) used in repeated choices that allow probabilistic tests of transitivity (set B).

Choices constructed using set A and set B stimuli were intermingled in each block. For both the art and chocolate bar brand categories, we designed option sets in which the options were normed to be close in preference. The gambles in the gamble categories are all of equal expected value (Supplementary methods).

Procedure. Participants completed a binary forced choice task. On each trial, participants first saw a central fixation point for 1s, then a screen with two choice stimuli (placed to the left and the right of the center). Participants indicated which stimulus they preferred, by pressing buttons for left or right. Participants had as much time as they needed to make their selection. Following their selection, there was an inter-trial interval of 1s where a black screen was presented.

For set A stimuli, participants faced all possible pairings of either 10 (for brands) or 11 (for art and gambles) options, constituting 45 and 55 pairs in total, respectively. Each pair was faced once. For set B stimuli, participants faced all possible pairings of 5 options, constituting 10 pairs, and each pair was repeated 15 times. Therefore, there were 195 (for brands) or 205 (for art and gambles) total choices in each category across the entire experiment.

Choice trials were presented in blocks, in which participants made choices between items within a single category (art, brands, gambles). There were five blocks of choices for each category, containing 39 (for brands) or 41 (for art and gambles) trials each. Each block contained 9 or 11 choices composed from set A and 30 choices composed from set B. Choices from set A and set B were intermingled with each other within a block, with the set A stimuli inserted into a block of B stimuli in positions randomly selected from a uniform distribution. We took a number steps to reduce any potential memory effects for choices constructed with set B stimuli. We designed the sequence of trials so that: (1) the same pairing was not repeated within a minimum of 3 trials; (2) the same stimulus rarely appeared on immediately adjacent trials (no more than 9 times throughout the entire experiment); and (3) when the same pairing was repeated the choices immediately preceding and following that pairing differed from its previous occurrence (to minimize contextual memory). Furthermore, the side on which stimuli were presented was counterbalanced across repetitions. Finally, we divided the experiment into two sessions, held on separate days for every subject except two (due to scheduling constraints). The two sessions were held on average 8.09 (sd = 11.73) days apart (excepting the two who were tested on the same day, the sessions ranged from 1 day to 57 days apart). We did not observe a significant correlation between the total number of choice cycles and days between the two sessions ($r = 0.24$, $p = 0.12$).

Statistical Analysis

Choice cycles. All data was analyzed with MATLAB (Mathworks). We used the set A choices to replicate previous studies which counted the number of choice cycles. We first determined the preference ordering within each category for each subject. The 10 or 11 options within each category were ranked according to how many times each was chosen by that subject. Then, for each trial, a choice was counted as cyclical if a lower-ranked item was chosen over a higher-ranked item. Following Henri-Bhargava, Simioni and Fellows (12), ties were maintained in the rankings (i.e., more than option could have the same rank) to provide a more conservative definition of cyclical choices. Because the cyclical choice counts are not normally distributed, we used non-parametric statistics to test for group differences. We used Kruskal-Wallis tests to detect effects between groups, followed by one-tailed Wilcoxon ranked sum *post hoc* pairwise tests as appropriate (as several previous studies have found increased cyclical choices after VMF damage, we had strong hypotheses about the direction of the results). To test for within-subject effects, we used repeated measures analysis of variance (ANOVA) on rank-transformed data for the omnibus test and Wilcoxon signed-rank *post hoc* tests as appropriate.

Tests of a stochastic model of transitivity. We used the set B choices to perform tests of a stochastic model of transitivity. We first obtained the proportion of choices (out of a possible total of 15 choices) for each of the 10 choice pairs afforded by all possible pairings of the 5 options in each category. We then tested the random mixture model of preference by noting whether the choices violated the linear ordering polytope (LOP) (14). The random mixture model states that a person's response comes from a probability distribution over all possible orderings of the stimuli. Thus, at any one time, preferences are transitive, but the transitive state that one is in can vary. The probability of a person choosing one option (X) over another (Y) in a binary choice is the sum of all the preference states in which X is preferred to Y. In a two alternative forced choice task, this is constrained by the triangle inequalities. For every distinct X, Y, and Z in a choice set:

$$P_{xy} + P_{yz} - P_{xz} \leq 1$$

Where P_{xy} denotes the probability of choosing X over Y, etc. For up to 5 options in a 2AFC task, satisfying the triangle inequalities, which together define the LOP, is necessary and sufficient for a set of choices to be consistent with the random mixture model.

For choice probabilities that did not satisfy the triangle inequalities, we used the Q-test (28) software to determine whether the data were significantly outside of the LOP. Q-test uses maximum likelihood estimation to find the goodness of fit of the data at each vertex in the polytope, using a chi-squared bar distribution with simulated weights (28, 29). Any subject with choices in a category that produced $p < 0.05$ in this test were considered as significantly violating the LOP and thus, the random mixture model of preference.

Drift diffusion modelling and analysis of reaction times. We calculated ranks of options similar to the method we used in the set A (deterministic transitivity) above, where the option that was chosen most often overall was ranked first, and the option chosen second-most was ranked second, etc., and broke ties by looking at which options were more often chosen more than half of the time in every pair (12). Three subjects still had tied ranks after this process, in one category each: two were HC subjects in the gambles domain, the other was a VMF subject in the Art domain. These subjects in these categories only are dropped from the drift diffusion modelling below.

We fit a drift diffusion model (19) to the choices and RTs from all set B choices for every other subject and category in our experiment. We modelled the decision process as a decision variable (DV) that increased linearly with a slope $d*v^{\alpha}$, where *d* was the drift rate, *v* was the value difference of the options (expressed as the absolute rank difference between the two items for that individual), and α was an exponent accounting for potential non-linearities in the effect of rank difference. We also assume that at each time step there is Gaussian noise added to the DV, with a standard deviation of ε. We assumed 10ms time steps. We also assume there is a non-decision time (*ndt*) before accumulation begins, and an initial value (*int*) of the DV that is constant across trials. Choices are made when the DV crosses a threshold.

Thus there are five free parameters: *d,* α, ε, *int* and *ndt*. Note that the threshold was a fixed parameter across subjects, as one of the threshold, *d*, or ε must be fixed for the other two parameters to be estimable. We chose to fix threshold after a model-comparison process showed that option to provide the best model fits. Threshold was held constant at (+/-) 0.15. Values for *d* are sampled between 0 and 1, for ε are sampled between 0 and 1, for α are sampled between 0 and 3, for *int* are sampled between the threshold bounds, and for *ndt* are sampled between 0 and the minimum RT minus 10ms for that subject.

To fit these free parameters, we first calculated the cumulative probability that the DV crossed the threshold for the subject's choice (T_{correct} or $T_{\text{incorrect}}$, where "correct" was defined as choosing the option of higher rank) across all time steps. For each trial, we then calculated the joint likelihood of the subject's choice at the time which they made that choice (their trial RT, minus *ndt*), by taking the derivative of this cumulative probability at the timestep of the subject's choice (every 10ms to the maximum RT for the subject). The model was then fit using the MATLAB function *fmincon*, where the cost function was defined as the sum of the negative log likelihoods of the instantaneous probabilities of the subject's choices and RTs in all trials. The fitting procedure was repeated 10 times for each subject, with each iteration varying in randomly sampled starting values for the free parameters as specified above; the parameters with the lowest log likelihood out of the 10 was taken for that subject. The model was fit individually to each of the three reward categories (art, brands, gambles) for each subject.

To look at differences in DDM parameters between groups across categories, we performed a mixed ANOVA on each of the free parameters, with group as the cross-subject factor and reward category as the within-subject factor.

Acknowledgments: We would like to thank Avinash Vaidya and Arthur Lee for constructive discussion on aspects of data analysis. We would also like to thank Lesley Fellows for facilitating access to participants in Montreal, Christine Déry and Eileen Cardillo for coordinating participants in Montreal and in Philadelphia, and all of the participants themselves, without whom this work would not be possible. This work was supported by National Institute on Drug Abuse (NIDA) R01-DA029149 to JWK and an Natural Sciences and Engineering Research Council (NSERC) postgraduate doctoral scholarship to LQY.

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Legends

Figure 1. Overlap images of the VMF and frontal control lesion groups. Numbers below slices indicate the MNI z-coordinates. Colors indicate extent of overlap. L = left; R = right.

Figure 2. Participants with VMF lesions make more choice cycles. a) Group average and individual choices cycles in set A across all domains. Dots encircled in gray denote the VMF subjects whose number of cyclical choices were significantly higher compared to the HC group, and whose lesion extents are depicted in b. Error bars are standard errors of the mean. * denotes $p < 0.05$. N = 43 individuals. **b)** Lesion tracings of the three individuals with VMF lesions who had significantly more cyclical choices compared to healthy control subjects, as determined by case-control t-tests. Red denotes areas where at least one of these subjects had a lesion; yellow denotes the areas where at least one of these subjects had lesions *outside* of all other lesion subjects. There was very little overlap in lesions within the three subjects (only maximally two out of three and only in a small number of voxels). Numbers below axial slices indicate the MNI z-coordinates.

Figure 3. Participants with VMF lesions have higher decision noise. a) DDM parameter fits: noise, drift rate, initial starting point, non-decision time, and alpha (exponent on rank distance). Error bars are standard errors of the mean. * denotes $p < 0.05$, *** denotes $p < 0.001$. N = 40 individuals. **b)** Histogram of reaction times of all choices by HC group (orange) and VMF group (blue). RTs of correct choices (defined as choosing the option with the higher average rank to

the participant) are on the right, and RTs of errors (defined as choosing the option with the lower average rank) are mirrored on the left. N = 4500 data points (from 30 individuals).

Tables

Table 1: Demographics of participants

Group (n)	Gender	Mean age (sd)	Education in yrs
VMF (13)	7F:6M	59 (15)	14
FC (10)	7F:3M	66 (8)	14
HC (20)	15F:5M	62 (8)	15

Table 2: Results of LOP analysis, by category

	Art	Brands	Gambles
Respondent	*p-value*	*p-value*	*p-value*
Individuals with VMF lesions			
1	✓	✓	✓
2	✓	✓	0.64
3	✓	✓	0.83
4	✓	✓	✓
5	✓	✓	✓
6	✓	✓	✓
7	✓	0.57	✓
8	✓	✓	✓
9	✓	✓	0.92
10	✓	✓	✓
11	✓	✓	✓
12	✓	✓	✓
Frontal controls			
1	0.2	✓	✓
2	✓	✓	✓
3	✓	✓	✓
4	✓	✓	✓
5	✓	✓	0.57

6	✓	✓	✓
7	✓	✓	0.48
8	✓	✓	0.36
9	✓	✓	0.14
10	✓	✓	✓
Healthy controls			
1	✓	0.71	**0.0016**
2	✓	✓	0.9
3	✓	✓	✓
4	✓	✓	✓
5	✓	✓	✓
6	✓	✓	✓
7	✓	✓	✓
8	✓	✓	0.95
9	✓	✓	**0.01**
10	✓	✓	0.55
11	✓	✓	✓
12	✓	✓	0.09
13	✓	✓	✓
14	✓	✓	✓
15	0.24	✓	✓
16	✓	0.87	0.27
17	✓	✓	✓
18	✓	0.36	✓
19	✓	✓	0.26
20	✓	✓	✓

Note: Each participant participated in choices for all three categories.
Checkmark indicates subject fulfilled triangle inequalities for that category. Significant violations of linear ordering polytope are marked in bold.

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Figures

Figure 1.

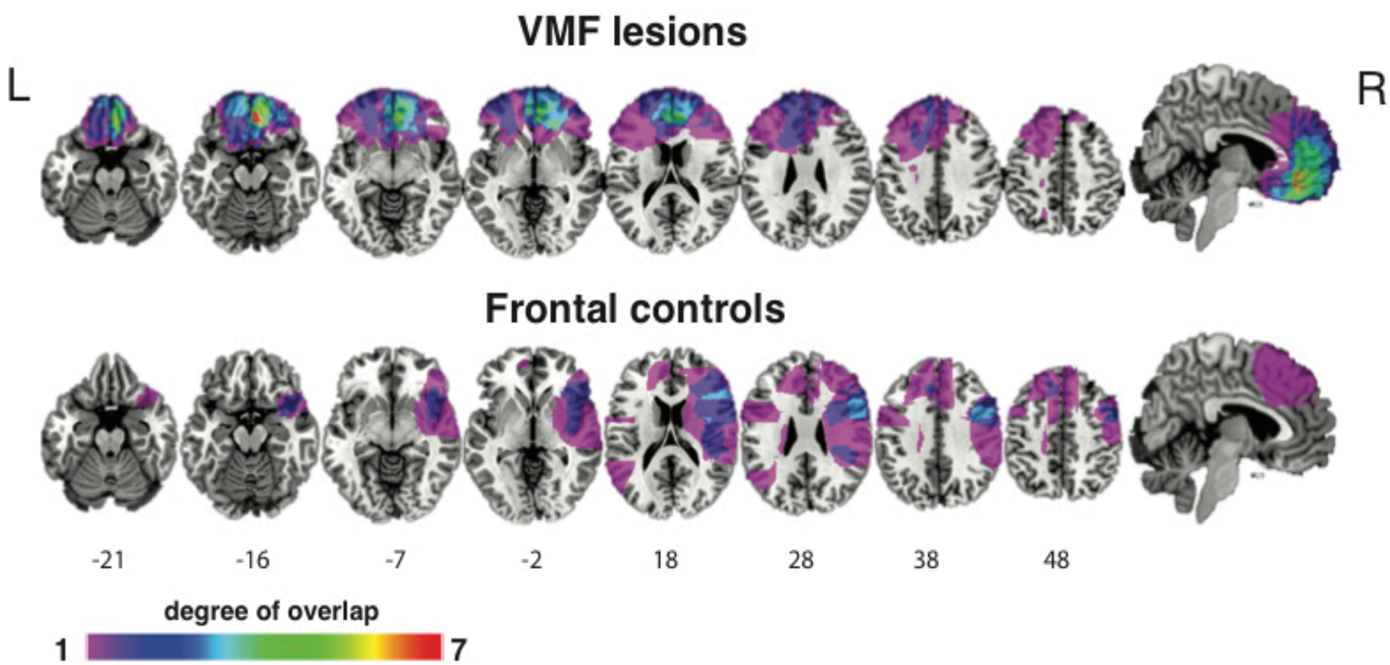
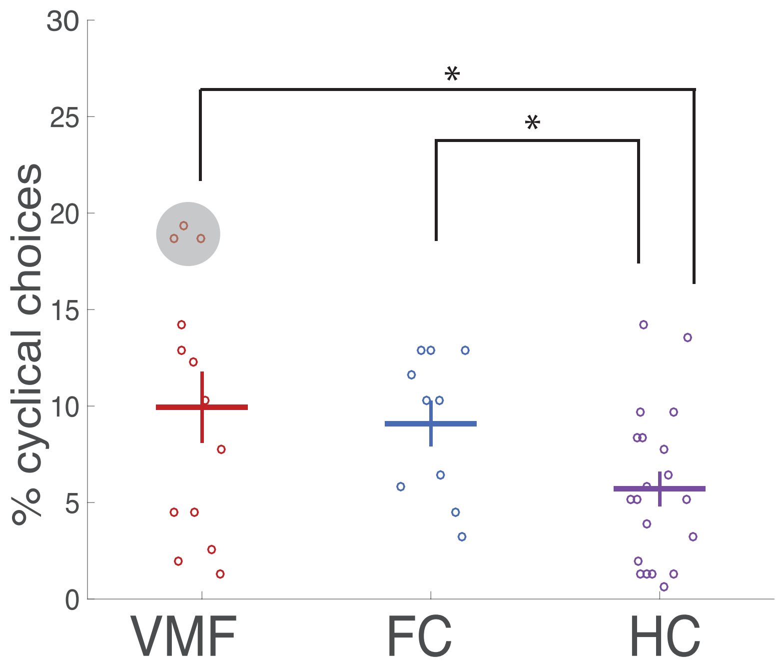


Figure 2.

A.



B.

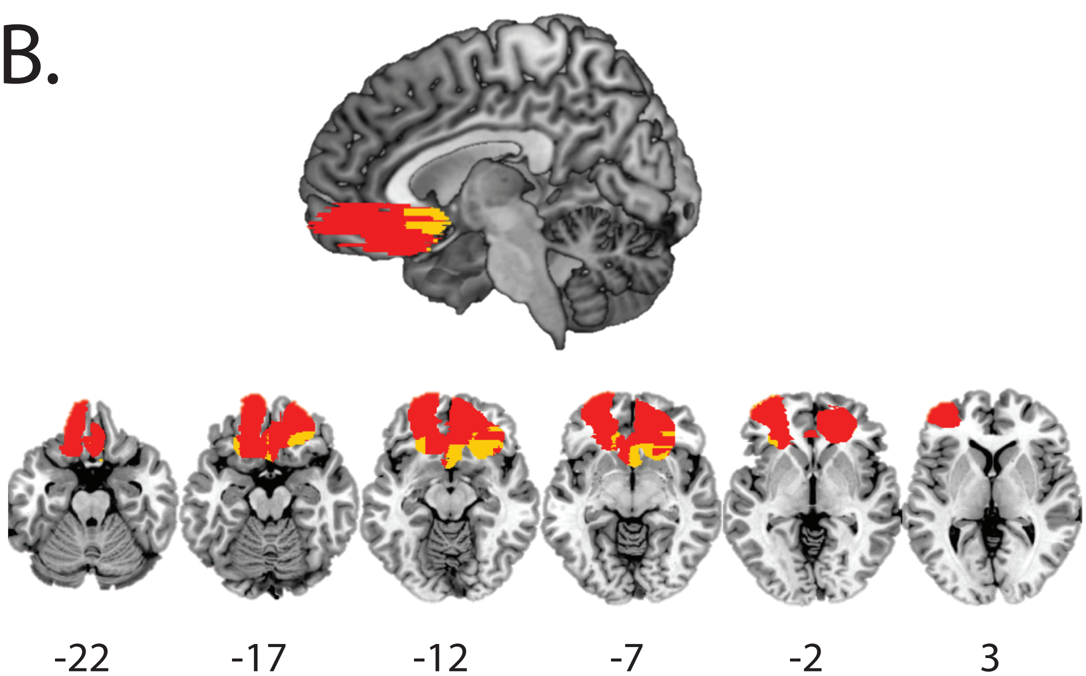
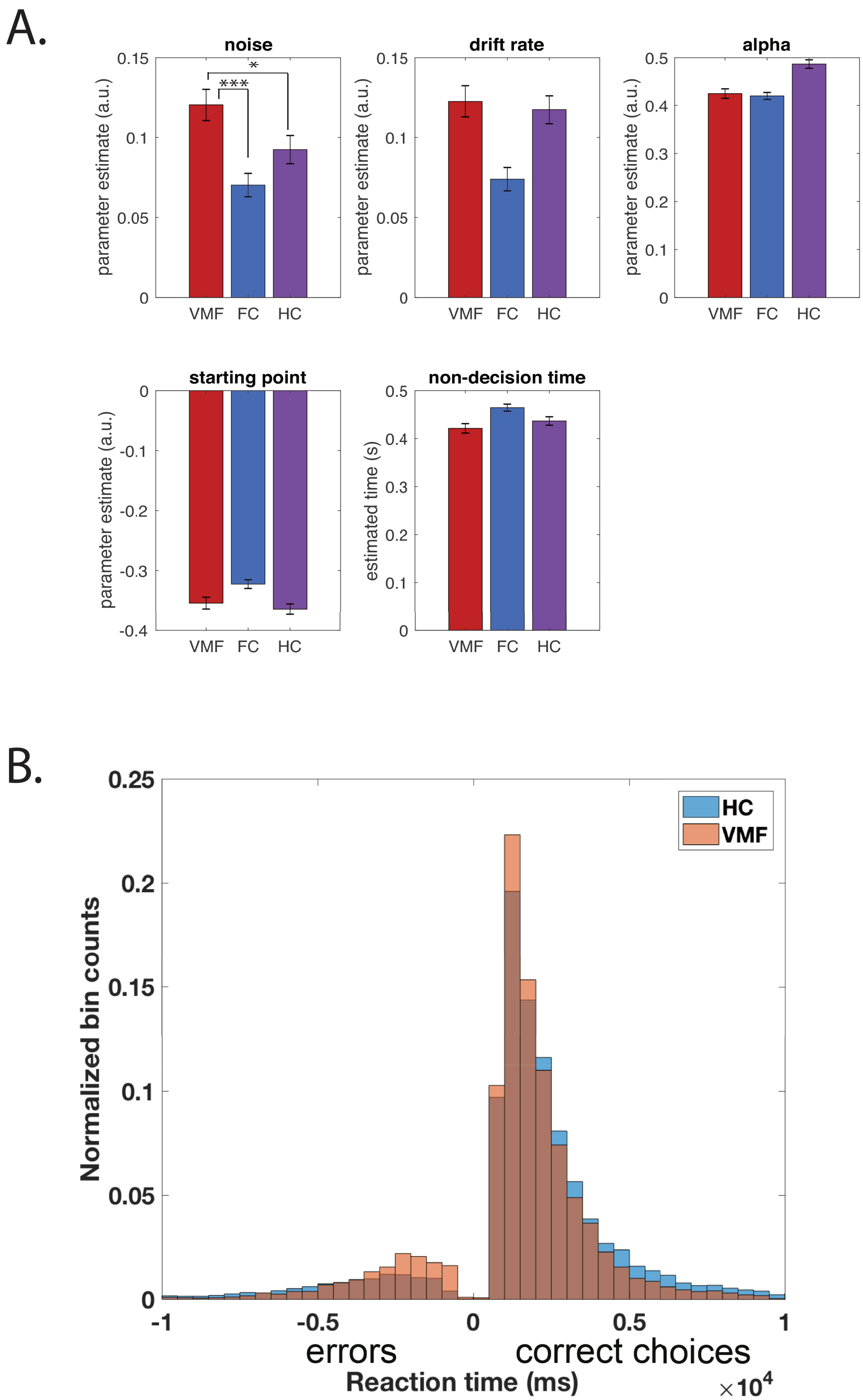


Figure 3.


A.
noise
drift rate
alpha
starting point
non-decision time
parameter estimate (a.u.)
estimated time (s)
VMF FC HC
*
***
B.
HC
VMF
Normalized bin counts
errors
correct choices
Reaction time (ms)
×10^4

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Supplementary Information for

Individuals with ventromedial frontal damage have more unstable but still fundamentally transitive preferences

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This PDF file includes:

- Supplementary methods
- Supplementary results
- Figs. S1 to S3
- Supplementary references

Supplementary methods

Stimulus norming. The artwork stimuli were paintings that were rated highly by participants in Vaidya and Fellows (1). The set B stimuli consisted of 5 paintings by Monet, which were all within the top 20 most highly rated paintings by those subjects. We selected Monet as he was the artist that occurred most frequently in the top 20 rated paintings of Vaidya and Fellows (1). The 5 selected paintings were roughly similarly preferred (i.e., chosen with close to the same frequency in pair-wise choices across the whole sample) in a sample of 107 participants recruited from Amazon Mechanical Turk. Set A consisted of paintings of the similar style/era (Impressionist, Romantic periods) in the top 40 ranked paintings of the Vaidya and Fellows (1) stimuli set.

The chocolate bars were from five brands (Lindt, Godiva, Ghirardelli, Dove, and Cadbury). We selected five brands that were roughly similarly preferred across the population. These brands were being sold for similar prices, were rated similarly on a seven-point scale by a sample of 103 participants from Amazon Mechanical Turk (mean rating = 5.76), and were selected at roughly similar frequencies in pair-wise choices across another sample of 101 Mechanical Turk participants. Milk chocolate bars from each of the 5 brands were in set B, while dark chocolate and dark chocolate almond bars from each brand were in set A. The stimuli consisted of publicly available pictures of the front side of the chocolate bar packaging.

We used sixteen gambles of equal expected value ($8.80). The stimuli consisted of a pie chart showing the probability of winning, with text on top indicating both the cash amount to be won and the probability of winning. The five set B gambles were the “Cash II” set in Regenwetter, Dana and Davis-Stober (2), which used contemporary monetary equivalents of the Tversky (3) five gamble set. The probabilities were 28%, 32%, 36%, 40%, and 44%. Set A consisted of 11 other gambles with the same expected value (probabilities of 8%, 17%, 25%, 33%, 42%, 50%, 58%, 67%, 75%, 83%, 92%).

Sensitivity of probabilistic tests. We performed several simulations to determine the sensitivity of tests of stochastic transitivity, i.e., the rate at which this test would declare different forms of random or heuristic-based choice to be intransitive. First, following Regenwetter, Dana and Davis-Stober (2), we randomly picked a choice probability for every pair from a uniform distribution (from 0 to 100%). As previously shown in that paper, only about 5% of the choice datasets simulated in this manner satisfy the triangle inequalities. That is, only 5% of the possible set of choice proportions for 10 pairs/5 stimuli satisfy the random mixture model.

Second, we simulated an intransitive chooser who has an entirely consistent preference within each pair (i.e., choosing A 100% of time when it is paired with B) that is unconstrained by any higher order transitive structure (i.e., the preference in each pair is independent from that of all other pairs). This type of intransitive chooser only satisfies the triangle inequalities about 12% of the time for choice proportions for 10 pairs/5 stimuli as in our dataset.

Third, we simulated an intransitive chooser using the lexicographic semiorder heuristic (3). This heuristic is easiest to demonstrate with the gambles stimulus set. Following Tversky (3), we defined our lexicographic semiorder rule as follows: if two gambles are adjacent (i.e., next to each other in the set in terms of probabilities/payouts), always choose the gamble with the higher payout (amount); for all other (non-adjacent) gamble pairs, always select the gamble with the higher probability. Such a chooser would never satisfy the triangle inequalities in our dataset. Together, the first three sets of simulations show that our tests of a stochastic model of transitivity are very sensitive to different forms of intransitive choice.

Finally, we simulated a completely random chooser (i.e., someone who flips a coin on every single trial). The choice proportions for such a random chooser are given by the binomial probabilities with p=0.5. Such a chooser satisfies the triangle inequalities 80% of the time in our dataset (5 stimuli, 10 choice pairs repeated 15 times). This high percentage is not unexpected, as 50% choice probabilities across all pairs is consistent with the random mixture model (i.e., 0.5 + 0.5 -0.5 < 1). We use this rate to assess whether the behavior of VMF subjects is consistent with completely random choice.

Supplementary Results

Differences among reward categories. We first examined how intransitive choices in set A differ across choice categories. In the one choice category used in previous studies of transitivity, art, there was significant difference in intransitive choices across groups (Kruskal-Wallis H = 7.62, p = 0.02), which replicated the previously reported pattern of selective VMF deficit. The VMF group (mean = 9.93%, sd = 1.86) made significantly more intransitive choices in the art category than both the FC group (mean = 4.73%, sd = 1.36; Wilcoxon ranked sum Z = 1.91, p = 0.03) and the HC group (mean = 3.64%, sd = 0.97; Wilcoxon ranked sum Z = 2.62, p = 0.004). In contrast, in the two categories that have not been used in previous studies, brands and gambles, we did not find significant differences between the three groups (brands, H = 2.42, p = 0.29; gambles, H = 3.01, p = .22 respectively).

The number of intransitive choices is relatively stable across categories in the VMF and HC groups, but variable across categories in the FC group (**Fig. S1a-c**). Indeed, the effect of reward category is significant for the FC group ($F(2,18) = 3.88$, $p = 0.04$), but not for the VMF ($p = 0.92$) or the HC group ($p = 0.27$). In the FC group, the number of intransitive choices in the gamble category was significantly greater than in the art category ($Z = 2.40$, $p = 0.02$), while the differences between gambles and brands ($p = 0.19$) and art and brands ($p = 0.18$) were not significant.

Category x Group effect on noise term in DDM. We were interested in whether the noise term might be higher for the VMF group in one category over the others. We performed a mixed ANOVA to see the effects of category (art, brands, gambles) and group on the noise term. We found that while there are main effects of group ($F(2, 37) = 6.25$, $p = 0.005$) and category ($F(2,4) = 12.85$, $p < 0.001$), there was no effect of interaction between category and group ($F(4,74) = 1.09$, $p = 0.37$). The main effect of group, as already explored in the main text, was driven by the higher noise term in the VMF group. The main effect of category is driven by the higher noise term in the art category (mean = 0.11) compared to both the brands (mean = 0.09) [$t(39) = 3.54$, $p = 0.001$] and gamble categories (mean = 0.08) [$t(39) = 3.96$, $p = 0.0003$)]. This result suggests that the while the art category produced higher decision noise for all participant groups, the VMF group was noisier consistently across every category (**Fig. S2**).

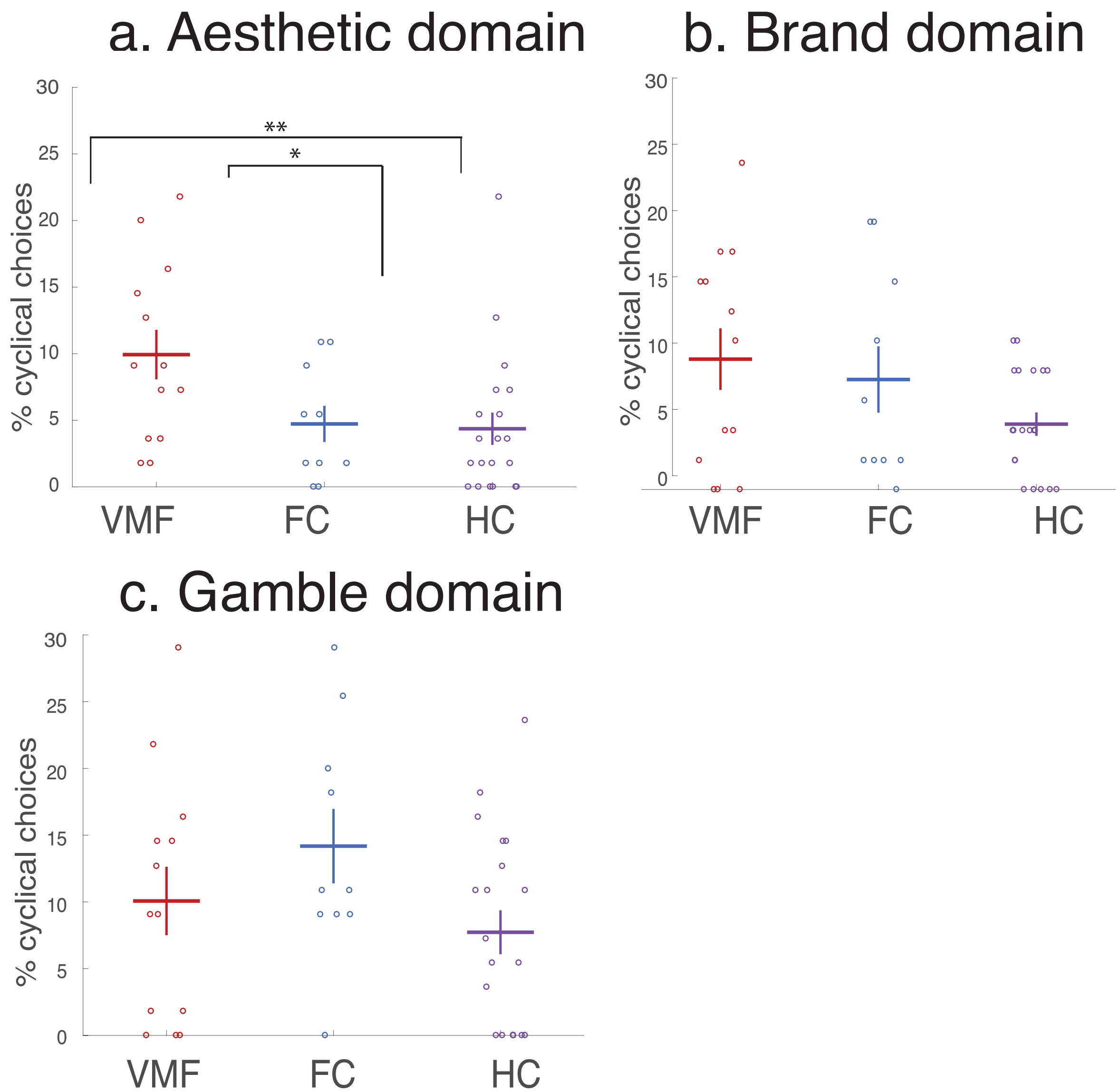

Fig. S1. Group average and individually plotted intransitive choices in (deterministic) set A for a) aesthetic, b) brand and c) gamble domains.

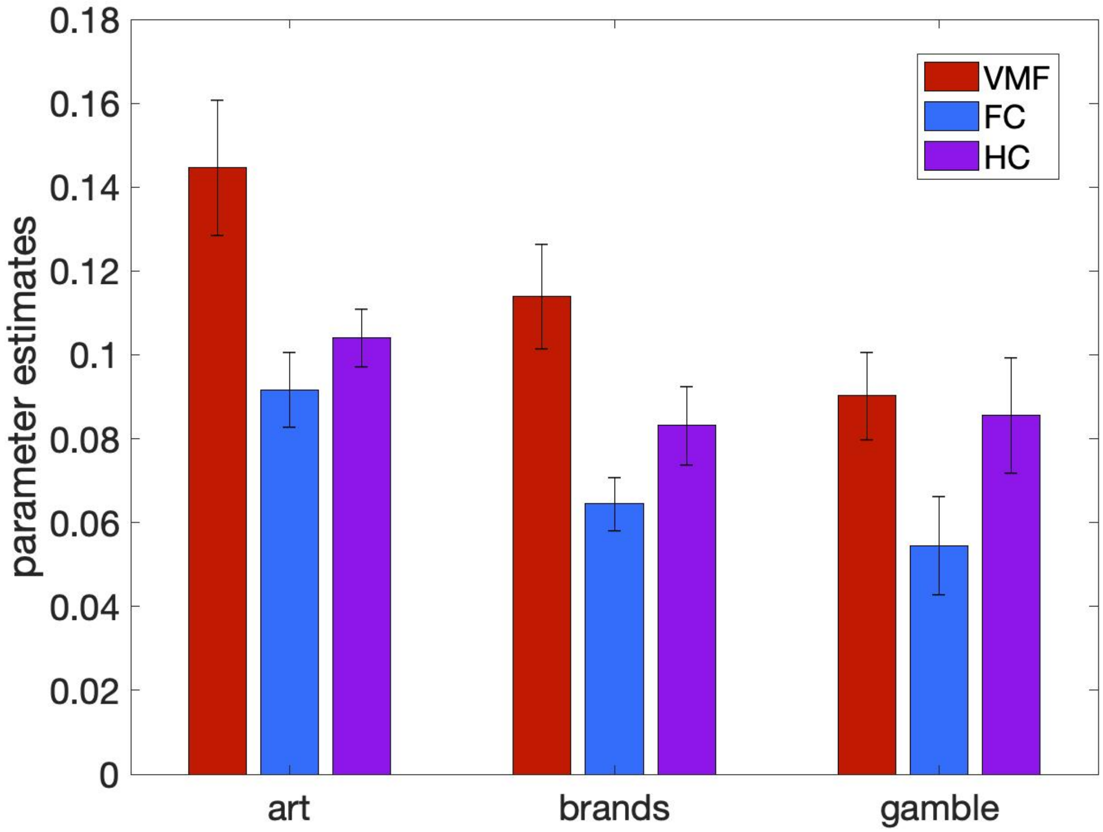

Fig. S2. The parameter estimates of the noise term in the DDM for each of the categories (art, brands, and gambles) for all three participant groups. Error bars are standard error of the mean.

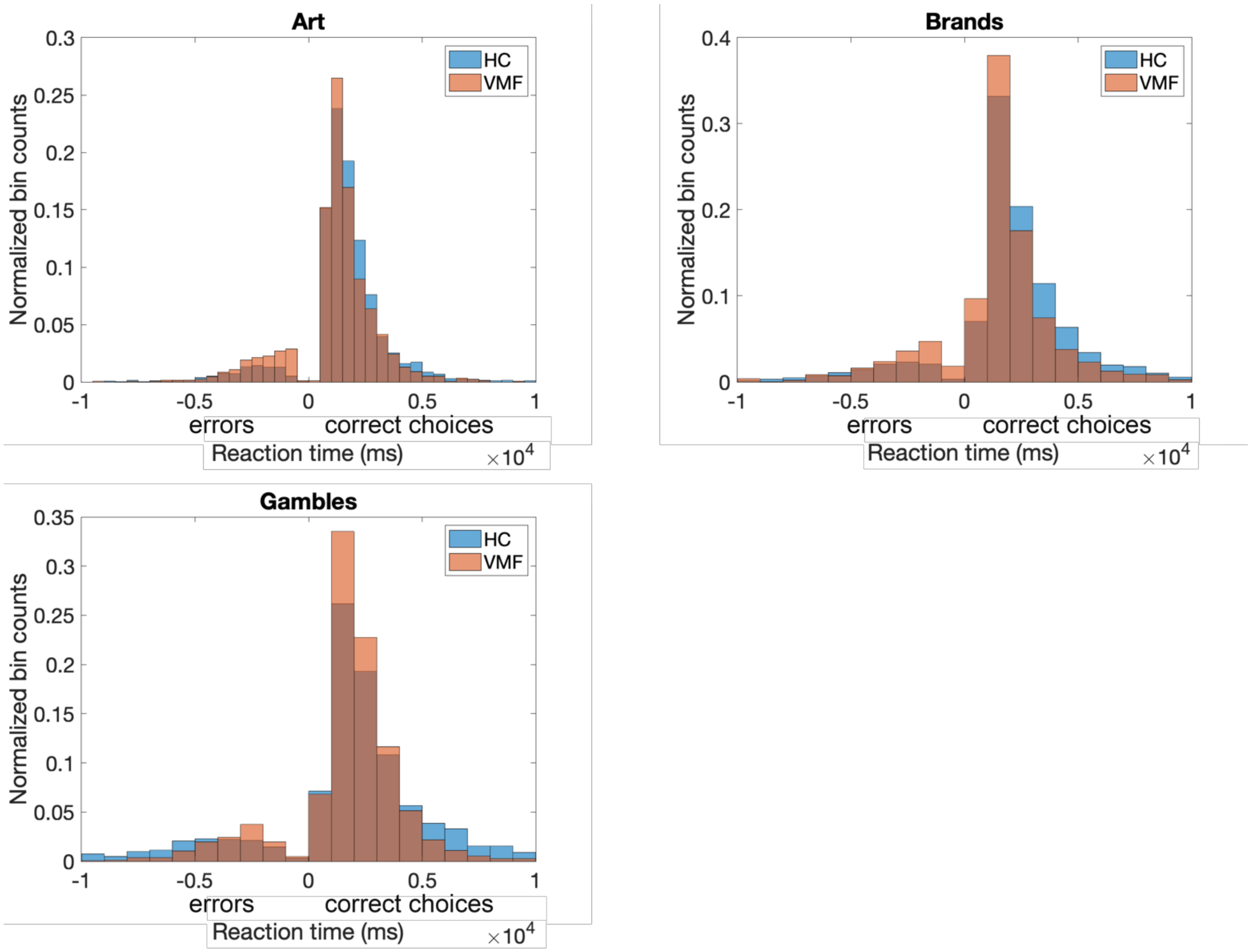

Fig. S3. The histogram of RTs for each of the categories for the HC and VMF groups. The error RT distribution is mirrored to the left (negatives), while the correct RT distribution is to the right (positives). These graphs illustrate that the VMF group (in orange) have a higher normalized count of fast error RTs in each category, a finding consistent with a higher noise term in the DDM.

Supplementary references

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