doi:10.1093/scan/nst187

SCAN (2014) I of I0

Neural basis of increased costly norm enforcement under adversity

Yan Wu,^{1,2} Hongbo Yu,² Bo Shen,² Rongjun Yu,³ Zhiheng Zhou,² Guoping Zhang,^{2,4} Yushi Jiang,⁵ and Xiaolin Zhou^{2,6,7}

Keywords: fairness; costly norm enforcement; ultimatum game; fMRI; computational modeling

INTRODUCTION

1998)
and the second
(i, 1958).
and the set of the second second second second second
(, , , , , , , , , , , , , , , , , , ,
(B <i>et al.</i> , 2003; <i>et al.</i> , 2006).
$\mathbf{A} = \mathbf{H}_{\mathbf{A}} + \mathbf{H}_{\mathbf$
$(1, \dots, 1) = (1, $
· · · · · · · · · · · · · · · · · · ·
i i i i i i i i i i i i i i i i i i i

Received 24 April 2013; Accepted 30 December 2013

Yan Wu and Hongbo Yu contributed equally to this work.

This study was supported by National Basic Research Program (973 Program: 2010CB833904), by grants from the Natural Science Foundation of China (30110972, 91232708, 71172216, 71132001, 31100744) and from the China Postdoctoral Science Foundation (20100470156, 2012T50023). Part of the findings reported in this article has been presented on the Peking University—New York University Joint Symposium on Neuroeconomics and Social Cognition (28–29 June 2010, Beijing) and on the Second International Conference on Neuroeconomics and Neuromanagement, Zhejiang University (27–28 October 2010, Hangzhou). The authors thank Ms Lihui Wang and Dr Luke Chang for neuroimaging data analysis, Ms Yunyan Duan for model estimation, and Mr Philip Blue and two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

Correspondence should be addressed to Xiaolin Zhou, Department of Psychology, Peking University, Beijing 100871, China. E-mail: xz104@pku.edu.cn

(et al., 2013), (et al., 2011); et al., 2011; et al., 2011), (et al., 2011); (et al.,
• • • • • • • • • • • • • • • • • • •
(D; <i>et al.</i> , 2004; B <i>et al.</i> , 2008). , (D; (D; (D; (D; (D; (D; (D; (D;

and the second
here he all a second a second
······································
· · · · · · · · · · · · · · · · · · ·
2007),
(i, B <i>et al.</i> , 2005; <i>et al.</i> , 2009; W
· · · · · · · · · · · · · · · · · · ·

, 2011). W

(et al., 2008; -266, et al., 2010).



Fig. 1 Sequence of events and timing in a trial. Each trial began by presenting the offer to the participant for 6 s. The participant was told to evaluate the offer but not to press any button at this moment. After a 2 s interval, the participant had to decide whether to accept or to reject the offer by pressing one of two buttons. After a nother interval, the duration of which varied from 1 to 3 s, the outcome of this trial was presented. Upon acceptance, the amount of gain or loss would be divided according to the proposer's offer. Upon rejection, both the participant and the proposer would get nothing (in the gain domain) or have to pain the full price (in the loss domain).

and the second
I the according to the second s
and the second
and the second state of the second state of the second
A (A : 10 10 10 10 10 10 10 10 10 10 10 10 10
A. A. S. C. S. C. C. S.
· · · · · · · · · · · · · · · · · · ·
1
A
(, 2, 8)
· · · · · · · · · · · · · · · · · · ·
and the state of the second
$\begin{array}{cccccccccccccccccccccccccccccccccccc$
· · · · · · · · · · · · · · · · · · ·
· • • • • • • • • • • • • • • • • • • •
· · · · · · · · · · · · · · · · · · ·
$\begin{array}{cccccccccccccccccccccccccccccccccccc$
$140 \dots 1 \sim 245 \dots E \qquad 1 \sim 1$
and the second

a na ana ang ang ang ang ang ang ang ang	-
$E = \frac{1}{60} + \frac{1}{$,
	, _
(1, 1, 2, 2, 3, 3, 4, 5, 5, 5, 5, 5, 5, 5, 5, 5, 5, 5, 5, 5,	
······································	-

fMRI data acquisition

F.		- 1			3		1.1	
			С	I	1	/	,	B

J	. 2			1.	
(48)		= 2400	K; $E =$	25.	;
$=90^\circ;$	$= 224 \times 224$	2;	1 = 3	× 3.5	× 3.5
³)					
· · · · · · · · · · · · · · · · · · ·	535	. i		· · ·	
· · · · · · ·					

Behavioral modeling

W		ser al en ser	· · · · ,	 (С.,
1968; F	/	, 199	99).	 A	1.1	1 2-1:
· · · · · · · · · · · ·	$\mathbf{A} = \{\mathbf{v}_i\}_{i \in \mathcal{N}}$					
			/			

$\cdots \rightarrow h $
(1, 2, 2, 2, 2, 2, 3, 2, 3, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3,
and the second
and the second
$\mathbf{H} = \mathbf{I} \cdot \mathbf{I} \cdot \mathbf{I} \cdot \mathbf{I} \cdot \mathbf{I} \cdot \mathbf{I} = \mathbf{I} \cdot $
$(1) \dots (1, 2), \dots (1, +, \dots, 1) \dots (1, -\dots) (1, -\dots)$
$(1 \dots 1) \qquad 11 = \dots 1 \dots $
$= \cdots + \cdots $
A second second have a second s Second second se Second second s Second second se
(P < 0.001)
$(\dots, P<0.01), \dots, (P<0.01), \dots, (P>0.01), \dots, (P>0.01), \dots, (P>0.01)$
(J
8 · 5-272.6 8 · · · · 69 () · · · · · · ((¹ / ₄))-3 (· · · 40 ·)-3 3.3 0 ·)-363 0 61 56.5 (0 63 ·)-314.3 (· · ·)-33 · · · · 3.0 61 · · · · · · 5 · 5 · · 3.3 · · · 7-476

. The here is a second second

Table	2	Brain	activations	in	the	aain	٧s	loss	contrast
Table	~	Diam	activations		uic	yam	22	1033	contrast

Regions	Hemisphere	Max T value	Cluster	Cluster level	MNI coordinates			
		1-Value	SIZE (VOXEIS)	conected P _{FWE}	x	у	Ζ	
Gain—loss								
VMPFC	R	6.85	155	<0.001	6	47	-11	
РСС	R	4.37	60	0.019	9	-10	-11	
VTA	L	6.73	167	<0.001	-6	—52	16	
Loss—gain								
Putamen	R	5.50	52	0.034	30	5	7	
DLPFC	L	7.01	138	<0.001	-36	2	34	
Rolandic	R	7.01	112	0.001	45	-10	22	
IPL/angular	R	5.32	153	<0.001	27	-61	46	
SOG	L	6.54	58	0.022	-21	-67	40	
Calcarine	L	8.15	554	<0.001	-18	-73	16	

SOG, superior occipital gyrus.

Table 3 Brain activations in parametric contrast (conjunction of gain and loss domains)

Regions	Hemisphere	Max T-value	Cluster size	Cluster level	MNI coordinates			
		/-value	(VUXCIS)	conected 7 FWE	x	у	Ζ	
Increase with SU								
VMPFC	L/R	4.55	181	0.021	6	53	—17	
VS	L/R	3.78	10	0.039 ^a	-3	8	-11	
Parahippocampus	R	4.02	151	0.044	18	-28	-10	
Fusiform	L	5.65	361	< 0.001	-33	-28	—19	
Precuneus	L	4.09	178	0.022	-9	-55	13	
Decrease with SU								
ACC	L/R	3.99	17	0.025 ^a	-6	32	25	
DLPFC	R	5.36	246	0.004	39	26	28	
	L	5.90	437	< 0.001	-42	20	31	
Putamen/insula	R	4.58	149	0.047	30	20	1	
PAG	R	5.12	278	0.002	3	-22	-14	
IPL	R	6.13	1342	< 0.001	24	-55	34	
	L	5.66			-24	-51	40	
IOG	L	4.60	674	<0.001	-42	—76	-8	

PAG, periaqueductal gray; IOG, inferior occipital gyrus. ^aSVC based on independently defined ROI (see Methods).

Y. Wu et al.

A, ACC,
D, FC,
$(\mathbf{F}_{i}, \mathbf{F}_{i}) = (\mathbf{F}_{i}, \mathbf{F}_{i})$
4)
3 3 3 4 5 5 5 5 5 5 5 5 5 5
(v_1, v_2, v_3, v_1) , (v_2, v_3, v_1) , $F_{(4, 68)} = 2.62, P < 0.05, v_2$
$t_{(17)} = 4.43, P < 0.001),$
(5:5; $t_{(17)} = -1.82$, $P = 0.087$).
······································
II and a second state of a second state of the second stat
r = 0.80
P < 0.001; E = 4C) (, et al., 2005).

Gain-loss domain modulates rejection-related activation in the dorsal striatum (DS)

(1, 1, 2, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3,
C
$P_{\rm C} = (-{\rm C}) < 0.05, k = 10; {\rm F} = 5{\rm A}$
$F_{\rm W} = \frac{1}{10000000000000000000000000000000000$
D
an 177 an ann a 177 a' an 777 an
 The second s
and a second contraction and a second s
and the second of the second second for the second s
n zana an an an zana an
$(1:9 \ vs \ 5:5) \qquad (1:9 \ vs \$
(c) and the second sec second second sec
αματικά το
W (vs , , ,) ,
\mathbf{D}
r = 0.67, P < 0.05; F = 5C).



١

1 in Downloaded from http://scan.oxfordjournals.org/ at Peking University on February 7, 2014

Table 4 Brain activations in parametric contrast (domain-specific activations)

Regions	Hemisphere	Max	Cluster size (voxels)	Cluster level corrected $P_{\rm FWE}$	MNI coordinates		
		7-value			X	у	Ζ
Positive association with SU only in gain domain							
VMPFC	L	5.02	378	<0.001	-6	62	1
Caudate	L	4.62	673	<0.001	—18	14	19
MTG	R	4.23	154	0.041	51	-22	-11
Fusiform	L	5.10	232	0.006	-60	—43	-8
Angular	R	5.16	182	0.020	60	-52	25
Negative association with SU only in loss domain							
LOFC	L	4.93	170	0.027	-48	47	1



Fig. 4 Negative effect of SU modulated by frame. (**A**) Whole-brain level exploratory analysis of the contrast 'Loss_ [masked (excl.) by Gain_]'. (**B**) Beta values corresponding to 10 types of offers (based on GLM 3) extracted from the DLPFC peak. (**C**) The difference in the mean beta values in the gain and loss domain predicted the differences in rejection rates between the loss and gain domain (r = 0.80, P < 0.001). ***P < 0.001 (two-tailed). Error bars represent s.e.m.

Gain-loss domain and third-party punishment	······································
a construction of the state of	· · · · · · · · · · · · · · · · · · ·
An art the state of the state o	$F_{(4,120)} = 48.87, P < 0.001$.
(1,1) + (1,1	$\cdots \mathbf{A} A$
(x, y, y) = (x, y, y) = (x, y, y) + (y, y) + ($F_{(1,30)} = 1.30, P = 0.264; A = 0.264; F_{(4,120)} = 1.03,$
and the second	P = 0.395.



Fig. 5 Neural effects of interaction between choice and frame. (**A**) ROI-based analysis of the contrast 'Loss (rej-acc)'. SVC revealed an activation cluster in the left DS, whose rejection-induced activation was higher in the loss compared with gain domain. (**B**) Activation timecourse extracted from a 6 mm sphere around the maximum coordinates indicates that this interaction effect was driven by the amplified activation difference in the loss relative to the gain domain. (**C**) The differences in beta estimates extracted from the activation maximum (Loss – Gain) predicted the increases in rejection rate in the loss relative to the gain domain. (**C**) The differences in beta estimates extracted from the activation maximum (Loss – Gain) predicted the increases in rejection rate in the loss relative to the gain domain (r = 0.67, P < 0.05). Note, the white and grey dots are outliers identified by robust regression and they are down-weighted in computing the correlation coefficients (Wager *et al.*, 2005).





DISCUSSION

1	and the second s	a ser en s		
• • • • •		$\dots = n \dots$	$(\mathbf{z}_1, \dots, \mathbf{z}_{n-1}) \in \mathbf{I}_{n+1}$	· · ·
· · · · · · · · · · · · · · · · · · ·	(t <i>et al.</i> , 2013) , 2011).	, subjective vali		
$H \to \mathbb{Z}^{-1}$			1	, <i>i</i>
		·W	and a second	-
		/		

a second s
and the state of the
· ····································
. All and the second
$\mathbf{D} (\mathbf{B} et al., 2007).$
B et al., 2008, 2012; et al., 2011; C et al., 2007; 2013), et al. (2013) et al., 2011; C et al., 2011; C
$(1, \dots, 1) = (1, $
1
(1 + 1 + 1) $(1 + 1)$
et al., 2002; i et al., 2008; et al., 2010).
$(\mathbf{H}_{1}, \dots, \mathbf{H}_{n}) \in \mathbf{H}_{1} \to \mathbf{H}_{2} \to \mathbf{H}_$
B
$(a_1,a_2,a_3,a_4,a_5,a_5,a_1,a_1,a_2,a_2,a_1,a_2,a_3,a_1,a_2,a_2,a_1,a_2,a_2,a_1,a_2,a_2,a_1,a_2,a_2,a_1,a_2,a_2,a_1,a_2,a_2,a_2,a_1,a_2,a_2,a_2,a_2,a_2,a_2,a_2,a_2,a_2,a_2$
and the second

Increased demand for fairness under adversity

<pre>a a a a a a a a a a a a a a a a a a a</pre>
(1,2,2,2,3,3,3,3,3,3,3,3,3,3,3,3,3,3,3,3,
1 11 μ. μ. κ. μ. το
D = FC (x = D = FC) x = x
$\begin{pmatrix} & \text{ot } al \ 2006 \end{pmatrix}$
D, FC = W, F =
a. I. Leeven and the second s second second sec
······································
here we have a difference between the second s
$\mathbf{D} = \mathbf{D} = $
$(x_1, x_2, \dots, x_n) = (x_1, \dots, x_n) + (x_1, \dots$
$\sum_{i=1}^{n} (i + i) = (i + i) + (i + i) = (i + i) = (i + i) + (i$
(C at al. 2013)
and here was a difference of a second and here exists and
$= \frac{1}{4} \mathbf{r}_{1} + \mathbf{r}_{2} \mathbf{r}_{2} \mathbf{r}_{1} + \mathbf{r}_{2} \mathbf{r}_$
$\dots \leftarrow \dots \leftarrow \mathbf{D} \to \mathbf{D} \to$
(B et al., 1999; C et al.,
2008; 1, 2011; A et al., 2012), A et al., 2012,
- در در ۱۰ (۱۰ (۱۰ (۱۰ (۱۰ (۱۰ (۱۰ (۱۰ (۱۰ (۱۰
A
(a) A second set of the second set of the second s second second seco
(E. et al.,
2012).
D
· · · ································
· · · · · · · · · · · · · · · · · · ·
$\mathbf{r} = \mathbf{i} + $
$(\cdot \cdot$
et al., 2010; C et al., 2013; et al., 2013),
n an
$(A_{i})_{i} = (a_{i})_{i} = $
n an ann an Anna Anna Anna Anna Anna An
$(1,1,2,\ldots,n,n) \in \{1,2,\ldots,n\} \in \{1,2,\ldots,n\} \in \{1,2,\ldots,n\} \in \{1,2,\ldots,n\} \in \{1,2,\ldots,n\} \in \{1,2,\ldots,n\}$
1 mar a series 1. a series of the series of

	· · · · · · · · · · · · · · · · · · ·	a =	· ·		/	 . /	
		$\gamma = H$	1 1.				
REFER	ENCES						
	(4000) 77			-			

- Journal of Neuroscience, 27(31), 8161–5.
- . Neuroimage, 76, 412–27.
- в Mapping, 33(6), 1452-69.
- 639-50.
- B , . . , D., . . , E. . , C., F . , E. (2011). D . . Nature Neuroscience, 14(11), 1468-74.
- B , , , D , , D. , F., , C , , D. , A.C. (1999). . Psychopharmacology, 142, 24–30.
- .
- · · -. Proceedings of the National Academy of Sciences of the United States of America,
- 100(6), 3531–5. B , ¹₁, C , , , , , E, , , , , , (2005). Advances in Applied Microeconomics, 13, 1–23.
- . The American Economic Review, 77(3), 243-50.
- B , , , , A , , C. , D , .E., . (2008). W Neuron, 60(5), 930–40.
- W. Neuron, 60(5), 930-40.

 C.
 , C.F. (2003). B

 Cognitive Sciences, 7(5), 225-31.

 C.
 , ..., A.g. (2013). g

 V. Neuron, 60(5), 930-40.

 C.
 , C.F. (2003). B

 Sciences, 7(5), 225-31.

 C.
 , ..., A.g. (2013). g

 V. Neuroscience, 8(3), 277-84.
- Journal of Neuroscience, 33(17), 7109–21.
- C ., , , A ., , A, B., . (2013). 3505-13.
-
- *Science*, *305*(5688), 1254–8. . Games and D Economic Behavior, 47(2), 268–98.
- E, A. B, B, F. (2012). Sciences, 279(1749), 4923-8.
- F , E., F, , . (2004). . Trends in Cognitive Sciences, 8(4), 185-90.
- Quarterly Journal of Economics, 114(3), 817–68.
- . Neuroimage, 77, 246–53.
- ą, 5(4), 414–23.
- , ., B. (1982). A , , , , , , , , , , , , , B. (1982). A W. Journal of Economic Behavior & Organization, 3(4), 367–88. , . ¹., . . , B. (2010).
- . Neuropsychopharmacology, 35, 4–26. , ., E , ., B , A., . . (2006). C ,
- . Science, 312(5781), 1767-70.
- . Science, 320, 1092–5.

- , . . (2012). 1. . -. . .
- , D., ..., B., B ..., Neuroscience and Biobehavioral Reviews, 35, and the second 786-98
- , D., J., . . , , . . . , . . , Einen , . . , C., , , A., F. , E. (2008).
- 1....
- , D., , , A., , , , , , , , , , , E. (2006). D . Science, 314(5800), 829–32.
- Neuroimage, 38(1), 203–11. 1.1
- . Nature Neuroscience, 12, 535–40.
- Journal of Experimental Social Psychology, 45(3), 505–14.
- , D. ., C. . , C. . (1968). Journal of Experimental Social Psychology, 4(1), 1–25.
- Neuron, 5b(1), 14–8. , , , F , , B. , W 1105–7.
- 'D . . , . . , A., . . , . (2007). Annals of the New York Academy of Sciences, 1104, 35–53.
- the United States of America, 99(8), 5669-74.
- , .A. (2006). C in Cognitive Sciences, 10(2), 59–63. ? Trends
- , .A. (2011). - <u>1</u> - -
- , D., W. . Proceedings of the National Academy of Sciences of the United States of
- America, 110(6), 2070–5. , F., , , , , , , , , , (2009). . Proceedings of the National Academy of Sciences of the United States of America, 106(1), 340–5.

- , . (1958). The Philosophical Review, \$7(2), 164–94.
- A, . (1971). A Theory of Justice. C , A: . Neuron, 35(2), 395–405. 1.1 . . 1
- . .D. (2011). and the second second
- . Neuropsychopharmacology Reviews, 36, 114-32.
- Journal of .11 Acres 640
- Neuroscience, 31(19), 7168–73. , .-. (1754/2011). The Basic Political Writings.
- , C . . .
- , A., ,, , .., A., , .A., <u>1</u>, ..., E., C. .., .D. (2003).
- Science, 300(5626), 1755–8. . Science, 300(5626), 1755-8. С. 1 **11** 1 1 1 1 1 1 1
- Science, 29, 2043-6. , B., ..., D., . (2007). . Nature Reviews
- Neuroscicence, 8(4), 300–11.
- $\begin{array}{c} \text{A.B.}\\ \text{Behavior, C.}\\ \text{A.S.}\\ \text{A.S.$
-=). Psychological Science, 19(4), 339–47.

- Science, 211(30), 453-8. *....* , A., D. (1991). . . . The Quarterly Journal of Economics, 105(4), 1039–61.
- , . .D.,, .C., ..., .C.,, . (2005). w
- , F, B , , , , , , , , , B , , . (. . . .). w
- , J.D., , , F. . . , D. , . . (2011). J
- , , , (2011). Journal of Neuroscience, 31(14), 5244–52.