

available at www.sciencedirect.comwww.elsevier.com/locate/brainres

**BRAIN
RESEARCH**

Research Report
**Brain activations reflect individual discount rates in
intertemporal choice**
Josep Marco-Pallarés^a, Bahram Mohammadi^{a,b}, Amir Samii^b, Thomas F. Münte^{a,b,c,*}
^aDepartment of Neuropsychology, Otto-von-Guericke University, Magdeburg, Germany^bInternational Neuroscience Institute, Hannover, Germany^cCenter for Behavioral Brain Sciences, Magdeburg, Germany

ARTICLE INFO

Article history:

Accepted 10 January 2010

Available online 18 January 2010

Keywords:

Individual difference

Delay discounting

Intertemporal choice

Functional magnetic resonance
imaging

Nucleus accumbens

Anterior cingulate cortex

ABSTRACT

Humans discount the value of future rewards following a hyperbolic function and thus may prefer a smaller immediate reward over a larger delayed reward. Marked interindividual differences in the steepness of this discounting function can be observed which can be quantified by the parameter k of the discount function. Here, we asked how differences in delay discounting behaviour are reflected by brain activation patterns. Sixteen healthy participants were studied in a slow event-related functional magnetic resonance imaging experiment at 3T. In each trial, participants had to decide between a smaller but immediately available monetary reward (ranging between 14 and 84 Euro) and a larger delayed reward (26 to 89 Euro; delay 5 to 169 days) by button press. Participants had the chance to receive the reward corresponding to one of their decisions at the end of the experiment. As expected, participants differed widely with respect to the steepness of their discount function. By contrasting decisions at or near the individual participant's indifference point (as determined by parameter k) with trials either well below or well above this point two different brain networks with opposing activation patterns were revealed: Trials below or above the indifference point were associated with activation in the ventral striatum and ventromedial prefrontal cortex, whereas decisions at the indifference point gave rise to activation in medial prefrontal cortex. The opposite effects in the two systems at individual indifference point were interpreted as a reflection of response conflict.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Time affects the value of money, food and other rewarding commodities. In choosing between a (smaller) immediate and a (larger) delayed reward both, humans and animals ranging from great apes to pigeons often tend to prefer impulsive choices for the smaller but immediately available reward (Amiez et al., 2006; Kalenscher et al., 2005; Kalenscher and

Pennartz, 2008). On the other hand, and crucial for human economic behaviour, we sometimes wait for the return on financial investments for years or even decades (Rosati et al., 2007).

Whereas standard normative economic theory (Strotz, 1956) predicts exponential discounting, empirical evidence in humans suggests that future gains are discounted in a hyperbolic or quasi-hyperbolic fashion (Frederick et al., 2003).

* Corresponding author. Department of Neuropsychology, Otto-von-Guericke University, Universitätsplatz, Gebäude 24, Postfach 4120, 39106 Magdeburg, Germany. Fax: +49 671 1947.

E-mail address: Thomas.muente@med.ovgu.de (T.F. Münte).

For example, according to Mazur (1984) the value of a reward decreases over time following a hyperbolic function:

$$V = \frac{A}{1 + kD}$$

where V is the present value of the delayed reward A after a delay D , and k is the delay discount rate.

Patience is a virtue that is not shared by all humans, however. High individual values of k in the equation above indicate preference for immediate values (impulsive, impatient behaviour) and a steep discounting function, whereas lower values are associated with the patient willingness to wait for the larger delayed reward. Steeper discounting functions are found in heroin (Kirby and Petry, 2004; Kirby et al., 1999), cocaine (Kirby et al., 1999), tobacco (Reynolds, 2004; Reynolds et al., 2004) and alcohol addicts (Mitchell et al., 2005; Petry, 2001a) as well as pathological gamblers (Petry, 2001b), disorders characterized by impulsive behaviour. Discounting rate also presents a wide intersubject variability in the normal population (Chabris et al., 2008) and the individual k -rate seems to be related to the impulsivity personality trait (Reynolds, 2006).

A number of previous studies have investigated the neural systems involved in delay discounting (Bickel et al., 2009; Boettiger et al., 2007; Engelmann and Brooks, 2009; Hariri et al., 2006; Kable and Glimcher, 2007; Luhmann et al., 2008; McClure et al., 2004, 2007; Peters and Buchel, 2009; Pine et al., 2009; Weber and Huettel, 2008; Xu et al., 2009). Interestingly, Hariri et al. (2006) found that the interindividual variability of the delay discount rate determined off-line in a behavioural task was correlated to activation of the ventral striatum in a guessing-reward task. Kable and Glimcher (2007) recently showed how individual subjective value of delayed gains was reflected by the activity of reward related brain areas (ventral striatum, medial prefrontal cortex and posterior cingulate cortex). Peters and Buchel (2009) contrasted delay and probabilistic discounting conditions in a recent fMRI study. In their study delayed and probabilistic rewards were discounted behaviourally in a hyperbolic manner with discount rates varying greatly between participants. Functional imaging data suggested that ventral striatum and orbitofrontal cortex are involved in coding of subjective value irrespective of whether rewards were delayed or probabilistic. Fronto-polar, lateral parietal and posterior cingulate cortex only correlated with the value of delayed rewards, whereas other regions were driven by the value of probabilistic rewards. This led the authors to propose that coding of subjective value in the human brain is based on the combination of domain-general and domain-specific valuation networks.

Building on these previous results, we examined the neural correlates of interindividual differences in delay discounting focusing on choices at or near the individual indifference point. Each individual's delay discounting parameter k can be determined from their choices (see Fig. 1). From an individual's k we can deduce for which decisions this particular person will be indifferent (e.g., an individual k -value of 0.06 implies indifference for the choice: "What do you prefer, 55\$ today or 75\$ in 61 days?").

Previous work has shown that "difficult" decisions in delay discounting tasks lead to an engagement of the medial prefrontal cortex including the anterior cingulate cortex (McClure et al., 2004; Pine et al., 2009). What is a difficult decision and

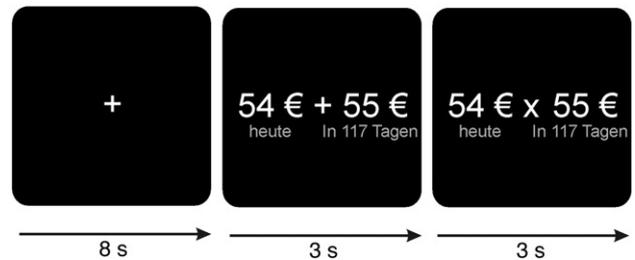


Fig. 1 – Experimental paradigm: First, a fixation ‘+’ sign appeared in the screen. After 8 s, the two options were presented. After an additional 3 s the fixation turned to an ‘x’ and subjects had to decide between one of the two options.

what is not, or, more precisely, which decisions lead to a conflict between the two possible options, should differ greatly between individuals as they also differ in the steepness of their discounting function. We therefore hypothesized that decisions at or near the individual indifference point, but not choices of either immediate or delayed rewards in trials far away from it, would engage the brain's conflict monitoring system located in the medial prefrontal cortex.

2. Results

2.1. Behavioural results

The mean delay discount rate (k rank) was 5.3 ± 1.2 . Fig. 2A shows the distribution of discounting values of the different subjects. The consistency (percentage of participant's choices that were consistent with their assigned discount rate) was

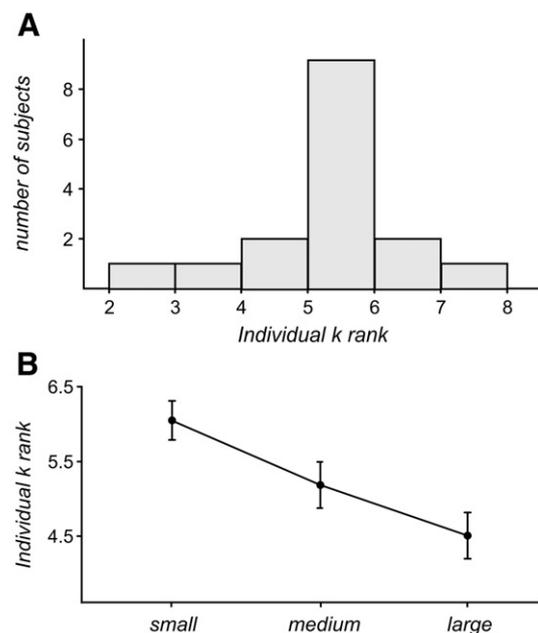


Fig. 2 – A. Histogram of the individual delay discount rates based on participants' responses. B. Delay discount rate according to magnitude of reward. Error bars indicate the standard error of the mean.

94±3%. There were no significant differences in consistency across the different runs (1st run: 92±7%; 2nd run: 94±4%, 3rd run: 94±4%, 4th run: 95±2%; $F(3,42)=1.9$, $P>0.1$). In addition, subjects presented greater delay discount rates for smaller than for larger rewards ($F(2,30)=13.4$, $P<0.005$, see Fig. 2B).

2.2. fMRI results

When trials with choices for immediate rewards and trials with choices for delayed rewards were compared to baseline very similar results ($P<0.05$ corrected for multiple comparisons, see Supplementary Figure 1) were obtained including activations of the anterior cingulate cortex, right and left insula, putamen (bilateral), left thalamus, superior parietal cortex and occipital visual areas. However, at the specified statistical threshold several contrasts did not show significant differences: (i) the comparison between choices presenting larger k -values and smaller k -values, (ii) the comparison between all choices of immediate and all choices of delayed rewards, (iii) the comparison between different reward magnitudes (small, medium, and large rewards, as specified in Table 1).

The main analyses took the individual k -value into account: At the individual participant level, a differential activation for several brain areas was observed when decisions close to the individual k -value were compared to all other decisions (see Supplementary Figure 2). In particular, when comparing

the choices corresponding to the two k -values nearest to the individual k -value, i.e. those decisions in which a participant is rather indifferent to both options (indifference, six decisions), with all other decisions (non-indifference) most participants presented a pattern characterized by an increased activation in medial orbitofrontal and subcortical areas (including the ventral striatum) for the non-indifference decisions, and increased activation in medial prefrontal/anterior cingulate cortex for the indifference decisions.

A multi-subject random-effects GLM of this contrast (using the individual k -values) revealed several consistently activated areas ($P<0.001$ uncorrected; see Table 2 and Fig. 3). Areas showing greater activation for the non-indifference trials included the Nucleus accumbens, Nucleus caudatus and ventromedial prefrontal cortex (vmPFC), i.e. areas that have been associated with reward processing. In addition, non-indifference trials also led to greater activation in the parahippocampal gyrus (PHG), the amygdala, several temporal areas and inferior parietal cortex.

The only area showing more activation for the choices close to the individual k -value was the medial frontal cortex (Fig. 3).

3. Discussion

Our experiment demonstrates the presence of two brain networks involved in the decisions for immediate and delayed

Table 1 – Choices presented in runs 1 and 3. SIR= small immediate reward, LDR = large delayed reward, k indiff = delay discounting value at which the two decisions are of equal subjective value, k rank = trials were ranked according to k indiff into 9 classes, LDR size = the size of the delayed reward was classified as small (S, between 25 and 35€), medium (M, between 50 and 60€) and large (L, between 75 and 85€). Note that in runs 2 and 4 trials were presented representing the same k -values but with slightly different absolute amounts (information given in Supplementary Table 1).

	Order 1st run	Order 3rd run	SIR	LDR	Delay (days)	k Indiff	k Rank	LDR size
1	13	22	34€	35€	186	0.00016	1	S
2	1	7	54€	55€	117	0.00016	1	M
3	9	26	78€	80€	162	0.00016	1	L
4	20	15	28€	30€	179	0.00040	2	S
5	6	2	47€	50€	160	0.00040	2	M
6	17	18	80€	85€	157	0.00040	2	L
7	26	9	22€	25€	136	0.0010	3	S
8	24	11	54€	60€	111	0.0010	3	M
9	12	23	67€	75€	119	0.0010	3	L
10	22	13	25€	30€	80	0.0025	4	S
11	16	19	49€	60€	89	0.0025	4	M
12	15	20	69€	85€	91	0.0025	4	L
13	3	5	19€	25€	53	0.0060	5	S
14	10	25	40€	55€	62	0.0060	5	M
15	2	6	55€	75€	61	0.0060	5	L
16	18	17	24€	35€	29	0.016	6	S
17	21	14	34€	50€	30	0.016	6	M
18	25	10	54€	80€	30	0.016	6	L
19	5	3	14€	25€	19	0.041	7	S
20	14	21	27€	50€	21	0.041	7	M
21	23	12	41€	75€	20	0.041	7	L
22	7	1	15€	35€	13	0.10	8	S
23	8	27	25€	60€	14	0.10	8	M
24	19	16	33€	80€	14	0.10	8	L
25	11	24	11€	30€	7	0.25	9	S
26	27	8	20€	55€	7	0.25	9	M
27	4	4	31€	85€	7	0.25	9	L

Table 2 – Summary of significant activations ($P < 0.001$, uncorrected), coordinates are given in Talairach space.

Region of activation	Laterality	Coordinates	Number of voxels	Cluster peak t value ($P < 0.001$)
		X, Y, Z		
<i>Non-indifference > indifference</i>				
Middle temporal	R	56, -14, -10	639	5.8
Insula	R	37, -1, 12	138	5.4
Superior temporal	R	52, -50, 15	508	5.2
Parahippocampal/amygdala	R	31, -8, -19	376	7.0
Ventral striatum/NAcc	R	3, 18, -1	1126	6.7
Ventromedial prefrontal cortex	R	2, 33, -10	155	4.4
Ventral striatum/NAcc	L	-8, 10, -4	239	5.1
Middle temporal	L	-49, -58, 12	2205	4.3
Insula	L	-36, -2, 12	160	5.0
Inferior parietal	L	-59, -31, 26	1806	5.9
Middle temporal	L	-56, -8, -10	396	6.2
<i>Indifference > non-indifference</i>				
Medial prefrontal	R	3, 14, 43	927	-5.7

rewards: one network is called upon when decisions concern immediate and delayed rewards of equal subjective value, while the other is engaged in situations in which either the immediate or the delayed reward clearly outweighs its alternative.

Interestingly, the brain activity in these two networks reflected the participant’s individual differences of the delay discounting functions. The network active in trials with a clear preference for either the immediate or delayed reward comprised limbic areas (including ventral striatum, ACC, and PHG and amygdala), vmPFC, temporal areas and the insula. In contrast, only one region was found to be activated for deci-

sions close to the individual indifference point, the posterior medial frontal cortex (pmPFC).

The activations found for non-indifference (clear preference) trials resemble results of recent studies on delay discounting. McClure et al. (2004), on the basis of economic theories, proposed the existence of two different systems: a “ β -system” comprising the ventral striatum, medial prefrontal cortex, and orbitofrontal cortex associated with choices involving immediate rewards, and a δ -system encompassing prefrontal and parietal regions which is thought to be active in all intertemporal choices, i.e. not just those decisions involving an immediate reward. The β -areas are typically

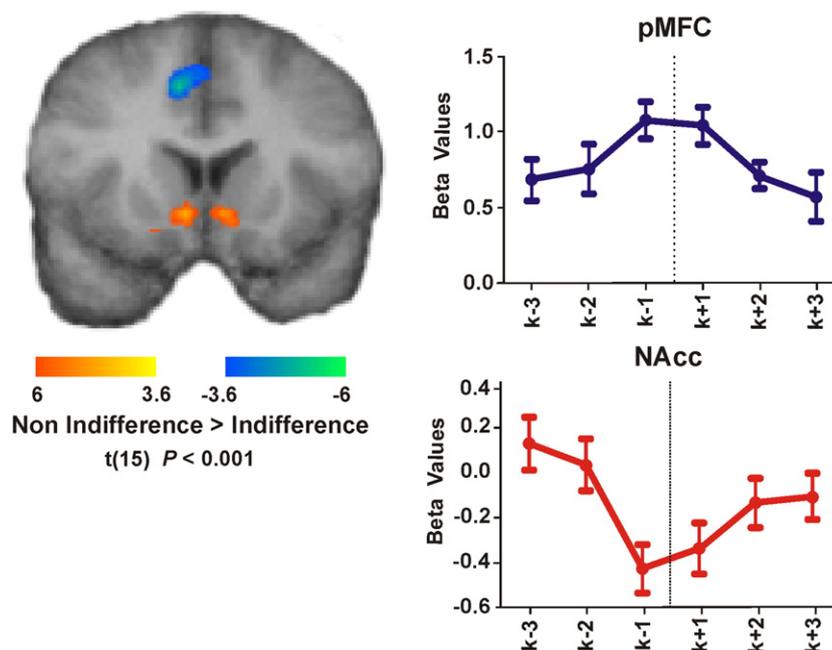


Fig. 3 – Areas presenting greater activity in the indifference condition (green/blue color scale; ACC) and non-indifference condition (red/yellow color scale; ventral striatum). The graphs show the activation of the ACC and striatum areas as a function of the k rank of the decisions with respect to the individual delay discount rate. Note the increase of activation of medial frontal cortex and the decrease of striatum in the indifferent conditions.

found in brain imaging studies involving reward processing (Delgado et al., 2000; Everitt and Robbins, 2005) or reward expectation (Knutson et al., 2005), and are sensitive to the reward magnitude and probability of reward (Knutson et al., 2005; Yacubian et al., 2006).

Turning to individual differences in delay discounting, Kable and Glimcher (2007) found that the activation pattern for the ventral striatum, medial prefrontal cortex and posterior cingulate cortex is compatible with the notion that these areas track the subjective value of delayed monetary rewards. Specifically, in their study activations increased when the objective amount of a reward was increased and decreased as a function of the delay until reward-delivery. These authors further demonstrated that behavioural trade-offs between reward amount and delay predicted the trade-off seen for the brain activation pattern on an individual basis. The non-indifference > indifference contrast of our study revealed brain areas that are very similar to the β system identified by McClure et al. (2004, 2007) and the brain areas studied by Kable and Glimcher (2007). The current analysis approaches the problem of individual differences from another angle, however. Interestingly, in our study the ventral striatum activation pattern was sensitive to the combination of immediate and delayed rewards as valued by the individual participant: combinations representing a k -value well below the individual's k for which the (subjective) value of the immediate rewards clearly outweighs the value of the delayed reward, as well as combinations representing a k -value well above the individual's k , equivalent to a subjective preference for the delayed reward, were associated with a higher activation than choices with about equal subjective value of immediate and delayed choices. In other words, the activity in the ventral striatum was smallest for choices close to the indifference point, even though in these cases, as in all others, participants eventually had to make a decision and were entitled to gains from these trials according to the payoff scheme.

In contrast to the rich pattern of activated areas in the non-indifference condition, only the posterior medial frontal cortex was found to be more active in the indifference condition. PMFC has been proposed to play a key role in performance monitoring by a plethora of neuroimaging studies (for review, Ridderinkhof et al., 2004). In particular, it has been pointed out that response conflict can drive activation in PMFC (Botvinick et al., 2001, 2004). Recently, Pochon et al. (2008) dissociated the decision and response phases of a complex decision task, and thus could demonstrate that the ACC does indeed reflect conflict at the decision stage. The present finding of an increased activation at the individual point of decision indifference is in line with the view of the PMFC as a conflict monitor. What we show for the first time in the context of intertemporal decision making is that its activity is driven by the steepness of each individual's discounting function.

Interestingly, McClure et al. (2007) in their study of time discounting of primary rewards identified a region in the dorsal anterior cingulate cortex (ACC) using an analysis designed to detect areas involved in the β -system. The authors interpreted the greater ACC activity in this context in the sense that choices involving an immediate reward option might be associated with greater conflict. More recently, Pine

et al. (2009) found anterior cingulate activity to be correlated with the degree of difficulty associated with dissonance between value and time further suggesting that the medial frontal activation in the present investigation might be related to the monitoring of conflict.

The present results demonstrate that there is a direct reflection of the steepness of the individual delay discount function in the pattern of brain activations in two systems, one related to the processing of rewards, the other sensitive to decision conflicts, during intertemporal choices. The finding of the opposing activation patterns in these two system leads to two suggestions for further research. First, further studies addressing delay discounting should take into account that decisions at or near the individual k -value are associated with differences in brain activations and therefore, depending on the specific question, should define contrasts based on individual behaviour or exclude trials near the indifference point. Second, the interaction of the two brain systems delineated in the present experiment should be studied in more detail using connectivity analyses (Camara et al., 2008; Gazzaley et al., 2007; Rissman et al., 2004; Stephan et al., 2007).

Obviously, the current study also has some limitations: the use of a convenience sample led to a clustering of individual k -values between k ranks 5 and 6 (Fig. 2A). An extension of the current study employing normal volunteers as well as pathological gamblers (defined as per DSM IV criteria) is currently underway which will allow to study more extreme discounting behaviour. Also, the individual discount rate as determined by the present method is the result of the individual balance of the tendency to go for immediate reward and the individual's capacity to control such tendencies, or, following McClure et al. (2004), the balance between β - and δ -systems. Thus, an individual may have a shallow discounting curve either because of a strong control system or because of a weak attraction to rewards. At present, we have no means to distinguish between these two possibilities.

4. Experimental procedures

4.1. Participants

Seventeen participants (11 women, all right-handed, mean age 28 ± 6 years) took part in the scanning session after giving their written consent. None of them had a history of neurological or psychiatric disorders. The experiment followed the Helsinki protocol and had been approved by the ethical committee of the University of Magdeburg.

4.2. Task

A version of the monetary-choice task devised by Kirby et al. (1999) was used. Participants took part in 4 runs, each with a fixed set of 27 choices between smaller immediate reward (SIR) and larger delayed reward (LDR; see Table 1). The order of trials within each run was arranged such that the trial order did correlate neither with the SIR or LDR amounts, nor with the temporal difference, delay or the discounting rate. Each trial began with a fixation cross (+) that lasted 8 s followed by the two choices which were displayed while the cross was

continuously present (e.g., “55€ heute+57€ in 117 Tagen”, “55 € today+57€ after 117 days”, see Fig. 1). After 3 s, the fixation cross changed to an “x”, and the participant was required to select the preferred option. Responses were performed with the index finger of the right hand on an MR-compatible response-pad, pressing the left button for left choice (in this case SIR) and the right button for the right choice (in this case LDR). Each participant received 7€ per hour for participation. In addition, in order to provide an incentive to perform the decisions as if they were real, participants were informed prior to the experiment that after the experiment they would have the chance of receiving the outcome of one of their 104 decisions. First they threw a dice. In case of a “six” they were allowed to draw a trial number. The participant’s decision was derived from the log-file of the experiment. If the participant had chosen the immediate reward, s/he received the sum in cash, in case of a choice for the delayed reward the sum was transferred to the participant’s bank account after the appropriate delay period. Of the 17 participants 4 received a reward. Stimuli were presented using MR-compatible video-goggles.

4.3. Behavioural analysis

The computation of individual discounting rate parameter (k -rate) was performed as described by Kirby et al. (1999), assigning a k -value to each subject that produces the highest proportion of choices consistent with that k -value. For example, a participant with a k -rate coinciding with the k of certain choice would be indifferent to this selection. For example, if s/he had a k -rate of 0.001, s/he would be indifferent to the selection 67€ now or 75€ in 119 days (Table 1). If s/he had a greater individual k -rate, s/he would select the immediate reward. Then, choices with the next k -value were examined (i.e., 49€ now or 60€ in 89 days, corresponding to $k=0.0025$). If the participant selected the delayed reward in this case, the individual k -rate was calculated to be the geometric mean of the two k -values, that is 0.0016.

We also computed the consistency of the k -rate (percentage of participant’s choices that were consistent with their assigned discount rate) over all trials to ensure that it reflected the general behaviour of participants and that it was consistent across the different runs.

4.4. MRI acquisition and analysis

We used a 3-T Siemens Magnetom Allegra Scanner to collect structural (T1-weighted MPRAGE: 256×256 matrix; FOV=256 mm; 192 1-mm slices) and functional images (EPI: TR=2000 ms; TE=30 ms; flip angle=80°; FOV=192 mm; matrix=64×64; slice thickness=3 mm; interslice gap=0.75 mm). Four runs of 193 functional images, each comprising thirty-four transversal slices covering the whole telencephalon, were obtained parallel to the anterior commissure–posterior commissure (AC–PC) plane.

fMRI data analysis included preprocessing (3D motion correction, slice scan time correction and temporal smoothing), co-registration and normalization to Talairach stereotaxic space using Brain Voyager QX. One subject was rejected from further analysis due to excessive movements. We per-

formed random-effects analyses on the z -transformed functional data. Different statistical analyses were performed under the General Linear Model (GLM). The first included the immediate versus delayed choices. The second compared the different magnitudes used (large, medium and small; see Table 1). Third we compared the brain areas activated as a function of the k -value of the pairs.

Finally we performed a GLM comparing the decisions under indifference versus the decisions in which subjects were not indifferent. To make this comparison, we selected for each subject and each run, the six choices that presented a k -value closest to the individual k -rate, and we compared these choices against the other pairs. For example, if the subject presented an individual k rank of 0.0098, for the first run the 13th to 18th choices in Table 1 were compared against the other choices. We make the assumption that the subject is indifferent to the two choices in these pairs, while the subject can make a clear decision (non-indifference) in the others. Statistical maps were created using a threshold of $P<0.001$ (uncorrected for multiple comparisons). All coordinates in the paper are given in Talairach space.

Acknowledgments

JMP has been a fellow of the Alexander-von-Humboldt Foundation and is supported by a Ramon y Cajal Grant. Supported by DFG-SFB 779, project A5, awarded to TFM. The authors declare that no competing interests exist.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.brainres.2010.01.025](https://doi.org/10.1016/j.brainres.2010.01.025).

REFERENCES

- Amiez, C., Joseph, J.P., Procyk, E., 2006. Reward encoding in the monkey anterior cingulate cortex. *Cereb. Cortex* 16, 1040–1055.
- Bickel, W.K., Pitcock, J.A., Yi, R., Angtuaco, E.J., 2009. Congruence of BOLD response across intertemporal choice conditions: fictive and real money gains and losses. *J. Neurosci.* 29, 8839–8846.
- Boettiger, C.A., Mitchell, J.M., Tavares, V.C., Robertson, M., Joslyn, G., D’Esposito, M., Fields, H.L., 2007. Immediate reward bias in humans: fronto-parietal networks and a role for the catechol-O-methyltransferase 158(Val/Val) genotype. *J. Neurosci.* 27, 14383–14391.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* 108, 624–652.
- Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn. Sci.* 8, 539–546.
- Camara, E., Rodriguez-Fornells, A., Münte, T.F., 2008. Functional connectivity of reward processing in the brain. *Front. Hum. Neurosci.* 2, 19.
- Delgado, M.R., Nystrom, L.E., Fissell, C., Noll, D.C., Fiez, J.A., 2000. Tracking the hemodynamic responses to reward and punishment in the striatum. *J. Neurophysiol.* 84, 3072–3077.

- Engelmann, J.B., Brooks, A.M., 2009. Behavioral and neural effects of delays during intertemporal choice are independent of probability. *J. Neurosci.* 29, 6055–6057.
- Everitt, B.J., Robbins, T.W., 2005. Neural systems of reinforcement for drug addiction: from actions to habits to compulsion. *Nat. Neurosci.* 8, 1481–1489.
- Frederick, S., Loewenstein, G., O'Donoghue, T., 2003. Time Discounting and Time Preference: A Critical Review. In: Loewenstein, G., Read, D., Baumeister, R. (Eds.), Sage, New York, NY, pp. 13–86.
- Gazzaley, A., Rissman, J., Cooney, J., Rutman, A., Seibert, T., Clapp, W., D'Esposito, M., 2007. Functional interactions between prefrontal and visual association cortex contribute to top-down modulation of visual processing. *Cereb. Cortex* 17 (Suppl 1), i125–i135.
- Hari, A.R., Brown, S.M., Williamson, D.E., Flory, J.D., de Wit, H., Manuck, S.B., 2006. Preference for immediate over delayed rewards is associated with magnitude of ventral striatal activity. *J. Neurosci.* 26, 13213–13217.
- Kable, J.W., Glimcher, P.W., 2007. The neural correlates of subjective value during intertemporal choice. *Nat. Neurosci.* 10, 1625–1633.
- Kalenscher, T., Pennartz, C.M.A., 2008. Is a bird in the hand worth two in the future? The neuroeconomics of intertemporal decision-making. *Prog. Neurobiol.* 84, 284–315.
- Kalenscher, T., Windmann, S., Diekamp, B., Rose, J., Gunturkun, O., Colombo, M., 2005. Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task. *Curr. Biol.* 15, 594–602.
- Kirby, K.N., Petry, N.M., 2004. Heroin and cocaine abusers have higher discount rates for delayed rewards than alcoholics or non-drug-using controls. *Addiction* 99, 461–471.
- Kirby, K.N., Petry, N.M., Bickel, W.K., 1999. Heroin addicts have higher discount rates for delayed rewards than non-drug-using controls. *J. Exp. Psychol.-Gen.* 128, 78–87.
- Knutson, B., Taylor, J., Kaufman, M., Peterson, R., Glover, G., 2005. Distributed neural representation of expected value. *J. Neurosci.* 25, 4806–4812.
- Chabris, C.F., Laibson, D.I., Schuldt, J.P., 2008. Intertemporal choice, In: Durlauf, S., Blume, L. (Eds.), *The New Palgrave Dictionary of Economics*, 2nd ed. Palgrave Macmillan, London.
- Luhmann, C.C., Chun, M.M., Yi, D.J., Lee, D., Wang, X.J., 2008. Neural dissociation of delay and uncertainty in intertemporal choice. *J. Neurosci.* 28, 14459–14466.
- Mazur, J.E., 1984. Tests of an equivalence rule for fixed and variable reinforcer delays. *J. Exp. Psychol. Anim. Behav. Process.* 10, 426–436.
- McClure, S.M., Laibson, D.I., Loewenstein, G., Cohen, J.D., 2004. Separate neural systems value immediate and delayed monetary rewards. *Science* 306, 503–507.
- McClure, S.M., Ericson, K.M., Laibson, D.I., Loewenstein, G., Cohen, J.D., 2007. Time discounting for primary rewards. *J. Neurosci.* 27, 5796–5804.
- Mitchell, J.M., Fields, H.L., D'Esposito, M., Boettiger, C.A., 2005. Impulsive responding in alcoholics. *Alcohol.-Clin. Exp. Res.* 29, 2158–2169.
- Peters, J., Buchel, C., 2009. Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. *J. Neurosci.* 29, 15727–15734.
- Petry, N.M., 2001a. Delay discounting of money and alcohol in actively using alcoholics, currently abstinent alcoholics, and controls. *Psychopharmacology (Berl)* 154, 243–250.
- Petry, N.M., 2001b. Pathological gamblers, with and without substance use disorders, discount delayed rewards at high rates. *J. Abnorm. Psychol.* 110, 482–487.
- Pine, A., Seymour, B., Roiser, J.P., Bossaerts, P., Friston, K.J., Curran, H.V., Dolan, R.J., 2009. Encoding of marginal utility across time in the human brain. *J. Neurosci.* 29, 9575–9581.
- Pochon, J.B., Riis, J., Sanfey, A.G., Nystrom, L.E., Cohen, J.D., 2008. Functional imaging of decision conflict. *J. Neurosci.* 28, 3468–3473.
- Reynolds, B., 2004. Do high rates of cigarette consumption increase delay discounting? A cross-sectional comparison of adolescent smokers and young-adult smokers and nonsmokers. *Behav. Process.* 67, 545–549.
- Reynolds, B., 2006. A review of delay-discounting research with humans: relations to drug use and gambling. *Behav. Pharmacol.* 17, 651–667.
- Reynolds, B., Richards, J.B., Horn, K., Karraker, K., 2004. Delay discounting and probability discounting as related to cigarette smoking status in adults. *Behav. Process.* 65, 35–42.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. *Science* 306, 443–447.
- Rissman, J., Gazzaley, A., D'Esposito, M., 2004. Measuring functional connectivity during distinct stages of a cognitive task. *Neuroimage* 23, 752–763.
- Rosati, A.G., Stevens, J.R., Hare, B., Hauser, M.D., 2007. The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* 17, 1663–1668.
- Stephan, K.E., Harrison, L.M., Kiebel, S.J., David, O., Penny, W.D., Friston, K.J., 2007. Dynamic causal models of neural system dynamics: current state and future extensions. *J. Biosci.* 32, 129–144.
- Strotz, R.H., 1956. Myopia and inconsistency in dynamic utility maximization. *Rev. Econ. Stud.* 23, 165–180.
- Weber, B.J., Huettel, S.A., 2008. The neural substrates of probabilistic and intertemporal decision making. *Brain Res.* 1234, 104–115.
- Xu, L., Liang, Z.Y., Wang, K., Li, S., Jiang, T., 2009. Neural mechanism of intertemporal choice: from discounting future gains to future losses. *Brain Res.* 1261, 65–74.
- Yacubian, J., Glascher, J., Schroeder, K., Sommer, T., Braus, D.F., Buchel, C., 2006. Dissociable systems for gain- and loss-related value predictions and errors of prediction in the human brain. *J. Neurosci.* 26, 9530–9537.