Journal Club

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The Role of the Medial Orbitofrontal Cortex in Intertemporal Choice: Prospection or Valuation?

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Review of Sellitto et al.

Many decisions only pay off in the future, requiring organisms to trade off between proximal and distal outcomes. Humans and many animals devalue rewards as a function of the time until their delivery, a phenomenon referred to as temporal or delay discounting. Several human functional magnetic resonance imaging (fMRI) studies have described the large scale neural networks involved in such intertemporal decisions (McClure et al., 2004; Kable and Glimcher, 2007; Peters and Büchel, 2010), and one region that is frequently found to be activated is the medial orbitofrontal cortex (mOFC). These studies have led to different proposed roles of the human mOFC in intertemporal choice. One prominent model, the beta-delta model, proposes that activation of a limbic network including mOFC and ventral striatum (beta system) increases the preference for smaller–sooner over larger–later rewards (McClure et al., 2004), whereas a prefrontal-parietal system (delta system) is thought to be involved in choosing larger but delayed rewards. In contrast, other models have suggested that mOFC, ventral striatum, and posterior cingulate cortex encode the subjective value of rewards across all delays (Kable and Glimcher, 2007). Of course, the necessity of regions that are shown to be activated in a given task cannot be inferred solely from neuroimaging data, and thus complementary lesion studies are required to establish the necessity of specific neural circuits. In rodents, lesions to the mOFC have been reported to increase temporal discounting (Rudebeck et al., 2006), whereas the effects of mOFC damage on temporal discounting in humans are unclear. Fellows and Farah (2005) observed no changes in temporal discounting following damage to the prefrontal cortex, but the lesions studied mostly included prefrontal regions more superior than the mOFC. Whether the mOFC plays a causal role in intertemporal decision-making in humans is thus an open question.

A recent report in the *The Journal of Neuroscience* addressed these important issues (Sellitto et al., 2010). Patients with focal lesions to the mOFC, non-mOFC lesioned control patients, and healthy controls completed temporal discounting tasks for different classes of hypothetical rewards: money, discount vouchers, and food. On each trial in these tasks, participants were required to choose between a fixed delayed reward (e.g., 40€ in 1 month) and a variable immediate reward. The immediate reward was adjusted dynamically until subjects were equally likely to choose each option. This procedure was repeated for six different delays to construct a discount curve that quantified the relationship between subjective reward value and time. Steeper discount curves reflect impulsive preferences (i.e., the individual prefers smaller–sooner over larger–later rewards), whereas more shallow curves reflect more patience (the individual is less impulsive and chooses larger–later rewards more often). A comparison of discount curves between subject groups showed that lesions including the mOFC were associated with a strong preference for immediate rewards, compared with non-mOFC patients and healthy comparison subjects. This effect was observed for all three classes of hypothetical rewards, and the authors replicated their findings in a subsample of patients and controls using real monetary payoffs. In addition, control analyses revealed that groups did not differ with respect to the degree of choice consistency such that the general shape of the discount curve did not differ between groups. A correlation between the degree of discounting and the lesion volume in area 11 was also observed, but given the small sample size this should be considered with caution.

These findings have direct implications for the ongoing controversy in the neuroscience of temporal discounting. If, as suggested by the beta-delta model (McClure et al., 2004), mOFC activation biases subjects to make more impulsive choices, inactivation of the mOFC would be expected to result in less rather than more discounting. However, the present data convincingly show an increase in temporal discounting following mOFC damage, as previously observed in rodents (Rudebeck et al., 2006). This is not easily reconciled with the beta-delta model, and therefore more compatible with an alternative model in which mOFC activity repre-

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sents reward value across all delays (Kable and Glimcher, 2007). Furthermore, the data strongly suggest that the human mOFC indeed plays a central role in intertemporal decision-making, thereby complementing previous functional neuroimaging studies and lesion studies in rodents.

Through what mechanism might the human mOFC contribute to temporal discounting? Two processes associated with this region immediately come to mind, both of which may contribute to intertemporal choice. First, mOFC is part of an extensive network, which also includes hippocampus, posterior cingulate cortex, and lateral parietal cortices, that is involved in episodic prospection, i.e., in the imagination of future episodes (Buckner and Carroll, 2007). Recent data indicate that people can use their ability to vividly imagine the future (a process consistently associated with mOFC activation) to attenuate impulsive discounting (Peters and Büchel, 2010). In particular, the more vividly future episodes were imagined, the more the subjective value of monetary rewards associated with these episodes increased. In the light of these findings, the data of Sellitto et al. (2010) are compatible with the view that lesions to (parts of) the episodic prospection network reduce the influence of episodic imagery on decision-making, thereby leading to an increase in impulsive choices. In support of this view, damage to another important node in this network, the hippocampus, reduces the ability to form vivid mental representations of novel experiences (Hassabis et al., 2007), and fMRI has recently revealed an association between hippocampal–prefrontal functional connectivity and the effect of prospection on intertemporal decisions (Peters and Büchel, 2010). In conjunction with the findings of Sellitto et al. (2010), these observations give rise to two predictions. First, one might expect mOFC patients to show impairments in future imagery, similar to patients with hippocampal damage (Hassabis et al., 2007); unfortunately, this was not examined in the present sample of mOFC patients. Second, hippocampal patients would be expected to show steeper temporal discounting, similar to the mOFC patients in the report by Sellitto and colleagues (2010). Testing both of these predictions would shed further light on the role of the prospection network in intertemporal decision making.

The role of the mOFC in encoding the subjective value of many different types of rewards might also contribute to intertemporal decision-making (Chib et al., 2009). Increased temporal discounting in mOFC patients was observed for a range of different reward categories, a finding in line with a domain-general role of the mOFC in reward processing. However, there is also evidence that different decision costs (such as temporal delays and effort requirements) may be processed in partially separate neural circuits. For example, ablation of rodent mOFC leads to a hypersensitivity to delays, but not to physical effort requirements (Rudebeck et al., 2006), compatible with recent human neuroimaging results (Prévost et al., 2010). The mOFC patients, on the other hand, were only tested on temporal discounting. It thus remains unclear whether mOFC damage in humans leads to a selective hypersensitivity to delays, or whether other types of decision costs are similarly affected. If the involvement of the mOFC in intertemporal choice is attributable to its role in episodic prospection, one could speculate that other forms of cost-benefit decision-making would be relatively unaffected (although prospection may play some role even in other domains). In contrast, if impulsive discounting following mOFC damage is due to a general valuation impairment, processing of other types of decision costs is likely to be affected as well. To more fully understand the contribution of the mOFC, it is therefore essential for future studies to explore the generality of the observed changes in decision-making in mOFC patients.

In summary, Sellitto et al. (2010) provide evidence for a prominent involvement of the human mOFC in intertemporal choice, and their findings are not easily reconciled with the beta-delta model. Candidate processes through which mOFC may exert its influence on temporal discounting have been identified (i.e., prospection and valuation), but their respective contributions remain unclear. Future studies are therefore required to assess whether mOFC damage-induced impairments in temporal discounting covary with changes in prospection, and whether mOFC damage leads to a more general impairment in cost-benefit decision-making that extends beyond the domain of intertemporal choice.

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