

Voluntary control of unavoidable action

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Goal-oriented behavior is usually portrayed to be directly related to incentive values. Underlying mechanisms are thought to include reward-oriented response bias and perceptual sensitivity. A recent electrophysiological study by Minamimoto *et al.* challenges this view, and reports neural activity in the thalamus that appears to counteract response bias. This type of activity might be crucial for our ability to engage voluntarily in actions that give little or no immediate return, but are necessary in the pursuit of long-term goals.

‘Nothing can oppose or retard the impulse of passion, but a contrary impulse; and if this contrary impulse ever arises from reason, that latter faculty must have an original influence on the will.’ [1] (p. 266)

The quote is from David Hume in *A Treatise of Human Nature*, but similar musings on the ability of individuals to restrain their desires and instead perform tedious, unpleasant and physically demanding tasks could easily be lifted from countless texts written by philosophers, poets and scientists in the last three or four millennia. More than one or two of these writers will even have asserted that the capacity for delayed gratification and long-term thinking is one of the secrets of our species’ success: humans know how to roll up their sleeves, and get the work done. Thanks to a recent report from Kimura’s laboratory [2] we now have a first glimpse of how the brain accomplishes this feat.

Goal-oriented control of action

In the past decade, a wealth of neurophysiological studies has concentrated on the key issue of ‘choosing the greater of two goods’ [3]. It is now well-established that midbrain dopamine neurons show an increased response to the presentation of reward-predicting stimuli [4], and this response appears to be monotonically related to the expected reward value [5]. Accordingly, the dominant view of the midbrain reward system is that the activity of dopamine neurons influences cortical and basal ganglia circuits for decision making and motor programming in such a way as to tip the balance in favor of actions that are associated with high incentive [6,7]. One illustration of how this system effectively orients behavior towards rewarding stimuli is provided by neurons in the caudate nucleus of monkeys that perform visually-guided eye movement tasks [8].

Figure 1a represents the typical activity of a neuron in the caudate nucleus, showing an increased firing rate in advance of eye movement instructions, but only in conditions when contralateral eye movements are associated with a large reward. Here, ‘contralateral’ means that the movement is in the direction opposite to the recording site (e.g. rightward eye movements for neurons in the left caudate nucleus). This anticipatory activity appears to create a response bias, prioritizing the planning of eye movements that promise a big return. Figure 1b depicts the implicated neural circuit. On this model the response bias in caudate nucleus emerges as the result of an interaction between cognitive information from cortex and reward-related dopaminergic input from the substantia nigra pars compacta [7,8]. The bias would then be propagated, via the substantia nigra pars reticulata, to neural structures that control movement.

Although the workings of this circuit might explain why rewarded eye movements are performed faster and more accurately than unrewarded eye movements, it can only be one part of a more complex system. As Minamimoto *et al.* dryly note, ‘an additional component, which plays complementary roles to response bias, seems to be required’ [2] (p. 1798).

Counteracting response bias

In some experimental situations, an individual might find herself forced to perform an action with little or no obvious incentive. For instance, in an operant-conditioning paradigm, a subject might have to complete small-reward trials in order to move on to the experimental session, and get access to large rewards in later trials. When a subject detects a stimulus associated with a small reward, a motivational conflict arises – a double bind in fact, as though the individual has to try to do voluntarily the thing she does not want to do. The situation does not match the response bias, and requires further mechanisms to disable any premature motor programming, either by inhibiting the now-irrelevant response bias, or by reinforcing the less-preferred but required action. By combining electrophysiological recording and stimulation techniques in such a paradigm, Minamimoto *et al.* [2] were able to identify neurons in the centromedian nucleus of the thalamus that are crucially involved in this opponent action.

In previous studies, the same researchers had encountered neurons in the centromedian nucleus – called ‘long-latency-facilitation’ or LLF neurons – that increased their firing rate in response to unexpected stimuli [9,10]. In the new study, LLF neurons were recorded while the monkey

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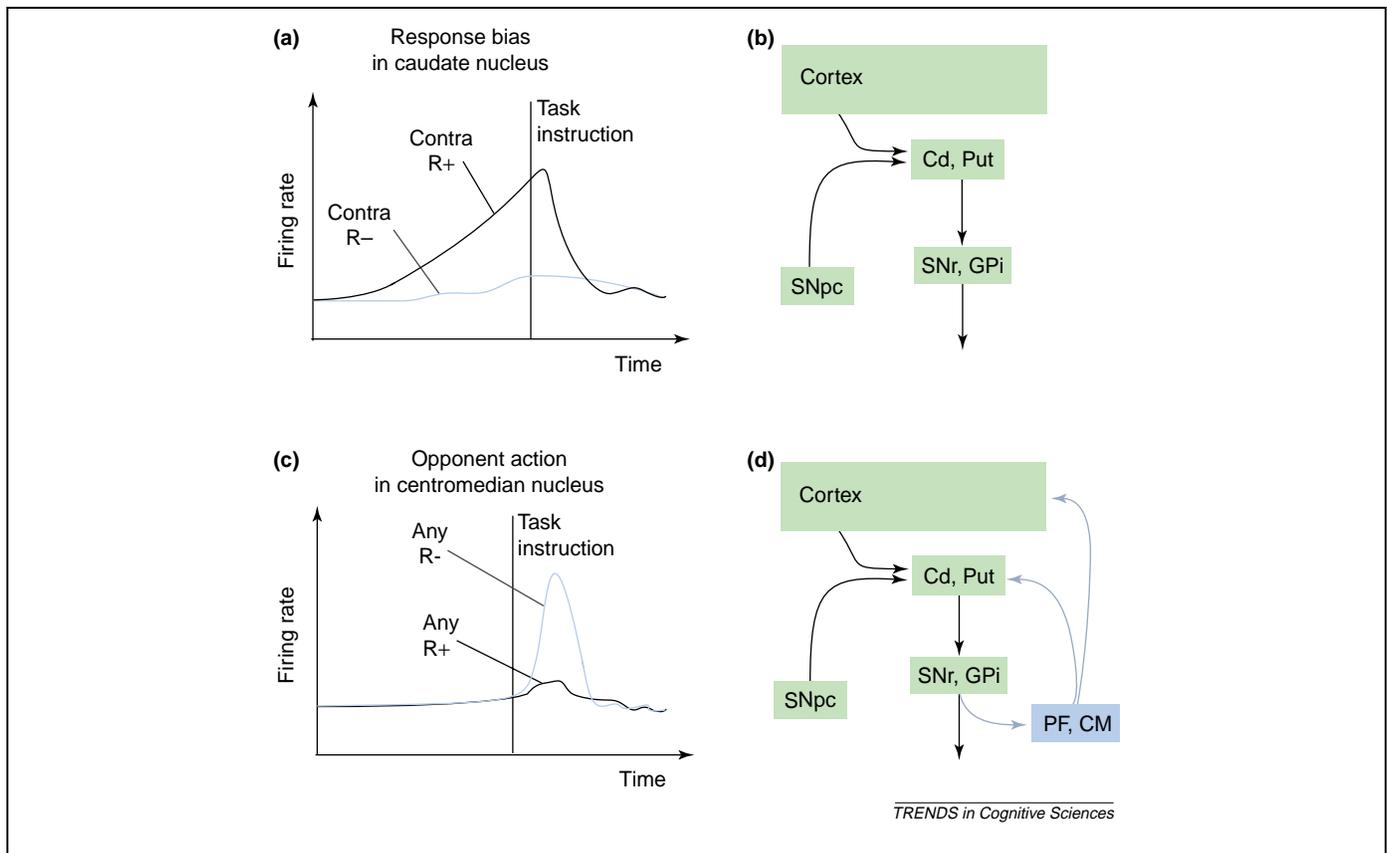


Figure 1. Neural mechanisms of voluntary control. (a) Response bias in caudate nucleus, seen as an increase of neuronal firing rate in advance of the onset of a task instruction. The increase occurs in conditions when contralateral movements are associated with a large reward (Contra R+, black line), but not in conditions when contralateral movements are associated with a small reward (Contra R-, blue line). (b) Neural circuit implicated in response bias. Caudate nucleus (Cd) and putamen (Put) are basal ganglia structures that receive glutamatergic input from cortex as well as dopaminergic input from substantia nigra pars compacta (SNpc). Cd and Put project to the basal ganglia output structures substantia nigra pars reticulata (SNr) and globus pallidus internal segment (Gpi), respectively. SNr and Gpi, in turn, influence the activity of neural structures that control movement. (c) Opponent action in centromedian nucleus, seen as an increase of firing rate after the onset of a task instruction, but only when the required action is associated with a small reward (Contra R-, blue line), not with a large reward (Contra R+, black line). (d) Neural circuit implicated in opponent action. In addition to the circuit in (b), SNr and Gpi project to posterior intralaminar nuclei of the thalamus: centromedian nucleus (CM) and parafascicular nucleus (PF). CM and PF, in turn, project back to the basal ganglia input structures, Cd and Put, in addition to cortical structures.

performed a manual GO/NO-GO task. Throughout a block of trials, either the GO or the NO-GO stimulus was associated with a large reward, and the other stimulus was associated with a small reward. Minamimoto *et al.* found that many LLF neurons show some very interesting properties (see Figure 1c). First, their physiological characteristics are a perfect complement to those of response-bias neurons in caudate nucleus. The LLF neurons respond with a burst of activity after stimulus presentation, rather than steadily building up to that moment. They also do not appear to be selective for the type of action required, responding to both GO and NO-GO instructions. Second, virtually all of the reward-sensitive LLF neurons in the centromedian nucleus showed a stronger response for small-reward than for large-reward stimuli. This observation stands in marked contrast to the results from studies of other brain areas [11–13], which reported only a minority of neurons with stronger responses to small-reward than large-reward stimuli. Thus, the activity seen in centromedian nucleus is emphatically not a mere duplicate of processes going on elsewhere in the brain. This new study, then, effectively puts the thalamus on the map as a key player in the motivational control of behavior, and modifies the standard model of the reward network (see Figure 1d).

Minamimoto *et al.* went on to show that the LLF neurons increase their activity still further in small-reward NO-GO trials depending on the likelihood of a large reward in the next trial, as if LLF neurons stimulate effort specifically when the long-term goal is in sight. If the neurons are active in these small-reward NO-GO trials, performance is highly accurate; if they are inactive, the monkey is more likely to make an error. Finally, by stimulating the centromedian nucleus during large-reward GO trials, the researchers found that reaction times were slowed – clear evidence that the normal mechanism of response bias was disrupted. All of these data converge on the notion that LLF neurons in the centromedian nucleus are crucially involved in counteracting response bias. In short, this part of the brain takes an important step in the control of unavoidable action.

A systems approach

Together, response bias and its opponent action would enable individuals to guide their behavior towards either proximal or distal goals, depending on the estimated costs and benefits. The implied flexibility in goal selection might indeed, as David Hume suggested, point to an effect of reason on the will. Whereas the mechanism of response bias would seem the natural starting point for any

individual, the opponent action might require a form of cognitive control. For instance, an individual might only reassess the situation, and consider different options, when she detects a mismatch between response bias and reward availability. Previous research has already suggested that the anterior cingulate cortex plays an important role in evaluating potential conflicts [14] and effort-related decisions [15]. Might the opponent action in centromedian nucleus in some way depend on input from anterior cingulate cortex?

Now that we have with a firm idea of what the neural signal for opponent action looks like, the obvious next question is how this activity depends on, or interacts with, other neural structures. The data cry out for a systems approach, examining the neurophysiological and neuropharmacological properties of the different projections. This can be done by simultaneous recording in multiple areas, combined with local electrical stimulation and/or administering of chemical agents. Much remains to be learned about how this system operates, but perhaps the most exciting message from the study of Minamimoto *et al.* is that we now already know at least one mechanism of goal-oriented control of action that is altogether different from the traditional story of dopamine, reward, and voluntary behavior. Researchers in the field will have to broaden their scope in order to understand fully how we manage to get so many difficult and unattractive tasks done.

References

- 1 Hume, D. (2000) In *A Treatise of Human Nature* (Norton, D.F. and Norton, M.J., eds), Oxford University Press

- 2 Minamimoto, T. *et al.* (2005) Complementary process to response bias in the centromedian nucleus of the thalamus. *Science* 308, 1798–1801
- 3 Sugrue, L.P. *et al.* (2005) Choosing the greater of two goods: neural currencies for valuation and decision making. *Nat. Rev. Neurosci.* 6, 363–375
- 4 Schultz, W. *et al.* (1997) A neural substrate of prediction and reward. *Science* 275, 1593–1599
- 5 Tobler, P.N. *et al.* (2005) Adaptive coding of reward value by dopamine neurons. *Science* 307, 1642–1645
- 6 Schultz, W. (2000) Multiple reward signals in the brain. *Nat. Rev. Neurosci.* 1, 199–207
- 7 Wickens, J.R. *et al.* (2003) Neural mechanisms of reward-related learning. *Curr. Opin. Neurobiol.* 13, 685–690
- 8 Lauwereyns, J. *et al.* (2002) A neural correlate of response bias in monkey caudate nucleus. *Nature* 418, 413–417
- 9 Matsumoto, N. *et al.* (2001) Neurons in the thalamic CM–Pf complex supply striatal neurons with information about behaviorally significant sensory events. *J. Neurophysiol.* 85, 960–976
- 10 Minamimoto, T. and Kimura, M. (2002) Participation of the thalamic CM–Pf complex in attentional orienting. *J. Neurophysiol.* 87, 3090–3101
- 11 Shidara, M. and Richmond, B.J. (2002) Anterior cingulate: single neuronal signals related to degree of reward expectancy. *Science* 296, 1709–1711
- 12 Kobayashi, S. *et al.* (2002) Influence of reward expectation on visuospatial processing in macaque lateral prefrontal cortex. *J. Neurophysiol.* 87, 1488–1498
- 13 Watanabe, K. *et al.* (2003) Neural correlates of rewarded and unrewarded eye movements in primate caudate nucleus. *J. Neurosci.* 23, 10052–10057
- 14 Brown, J.W. and Braver, T.S. (2005) Learned predictions of error likelihood in the anterior cingulate cortex. *Science* 307, 1118–1121
- 15 Walton, M.E. *et al.* (2003) Functional specialization within medial frontal cortex of the anterior cingulate for evaluating effort-related decisions. *J. Neurosci.* 23, 6475–6479

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Understanding the architecture of language: the possible role of neurology

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Culicover and Jackendoff have recently described an approach to language representation where semantic structure works, alongside syntax, as a generative system with its own structure and principles of composition. Well-known neurological observations support this view. They show that in the presence of a syntactic impairment, comprehension can take place but only if the sentence's semantic structure is rich enough. This would suggest the existence of syntax-independent semantic combinatorial mechanisms, as Culicover and Jackendoff's model proposes.

Sentence comprehension is one manifestation of linguistic composition. It results, in part, from lexicalized meaning coming together through at least one combinatorial system: (morpho-)syntax. Some of the information guiding (morpho-)syntactic composition, such as syntactic category, is also lexicalized. Nevertheless, syntactic categories are correlated with, but not definable by, meaning classes. Capitalizing on this insight, which is fundamental to most approaches to language representation, Culicover and Jackendoff [1] propose that these two kinds of information – syntax and semantics – are not only differentiated at the lexical level but are also deployed and manipulated via ‘parallel tracks’, as it were, at the phrasal and sentential

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