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Pupil dilations induced by barely conscious reward goal-priming

Yudai Takarada[a,*], Daichi Nozaki[b]

[a] Faculty of Sports Sciences, Waseda University, 2-579-15, Mikajima, Tokorozawa, Saitama 359-1192, Japan
[b] Graduate School of Education, The University of Tokyo, Bunkyo-ku, Tokyo 113-0033, Japan

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ABSTRACT

The topic of unconscious influences on behavior has long been explored as a way of understanding human performance and the neurobiological correlates of intention, motivation and action. Previous research using transcranial magnetic stimulation has demonstrated that barely visible priming of an action concept, when combined with reward in the form of a consciously perceived positive stimulus, can alter the state of the motor system and enhance the maximal voluntary force level. One possible explanation is that positive stimulus-induced reward signals are processed by the dopaminergic system in the basal ganglia, motivating individuals to increase the effort they invest in particular behaviors, or to recruit the resources necessary for maintaining those behaviors. If so, given that the dopaminergic system has functionally and anatomically close connections with the noradrenergic system, we hypothesize that the state of the noradrenergic system may be enhanced by the same process. In accord with this hypothesis, we observed that barely visible goal priming with reward caused pupil dilation, suggesting that activity in the noradrenergic system increased. Importantly, this enhancement was accompanied by an unconscious increase in handgrip force. This is the first objective evidence that the pupil-linked neuromodulatory system is related to implicit learning of the link between physical exertion and reward, probably in the noradrenergic system, resulting in more forceful voluntary motor action in the absence of conscious awareness.

1. Introduction

Motor actions are typically consciously controlled and managed. However, some situations require unconscious decision-making processes. Indeed, healthy individuals sometimes pursue behavioral goals unconsciously (Bargh et al., 2001), and when accompanied by a positive reward signal, this can enhance motivation to produce more forceful actions, independently of any reported increase in motivation to attain goals (Aarts et al., 2008). Such positive stimulus-induced reward signals are processed by the ventral pallidum (VP) in the basal ganglia, motivating individuals to increase the effort they invest in particular behaviors, or to recruit the resources necessary for maintaining those behaviors (Pessiglione et al., 2007). A recent electrophysiological study using transcranial magnetic stimulation indicated that barely visible goal-priming with motivational rewards increased corticospinal excitability, possibly leading to an enhanced maximal level of voluntary force exertion and submaximal force output (Takarada and Nozaki, 2014). We speculated that the reward-linked dopaminergic system may have been involved in the enhancement of the motor system by the positive stimulus-induced reward signal. However, this possibility has not yet been validated experimentally.

The dopaminergic system may function in conjunction with the noradrenergic system in regions with common projections. For instance, noradrenaline and dopamine can be released simultaneously in the prefrontal cortex (PFC), where they can function together to modulate network activity, mediating cognition in the area (Sara, 2009). The sole source of noradrenaline is from neurons in the locus coeruleus (LC) in the brainstem. LC activation does not affect neurons in the ventral tegmental area (VTA) that project to the nucleus accumbens (NAc), which is involved in dopamine release, but neurons in the PFC also project indirectly to the VTA. Accordingly, LC activation enforces interactions between the noradrenergic and dopaminergic systems, and the systems' mutual connections to the PFC (Sara, 2009). On the basis of these functionally and anatomically close connections between the noradrenergic and the dopaminergic systems, we hypothesized that the noradrenergic system state may also be enhanced by unconscious goal pursuit.

A number of studies have reported that pupillary dilation is associated with mental effort (cognitive load), and the correspondence between cognitive load and pupillary dilation has been documented in several contexts, including paired-associate learning (Colman and Paivio, 1970; Kahneman and Peavler, 1969) and imagery tasks with

* Corresponding author.
E-mail address: takarada@waseda.jp (Y. Takarada).

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abstract and concrete words (Paivio and Simpson, 1966, 1968; Simpson and Paivio, 1968). The size of the pupil at any time during a cognitive task reflects the subject's involvement in the task, and the precision of these changes has been found to enable the second-by-second analysis of task-load and mental effort (Kahneman and Beatty, 1966). Pupil dilation is controlled by the release of noradrenaline from the LC through α2-receptors, and has been used extensively as an indirect measure of LC activity (Phillips et al., 2000; Aston-Jones and Cohen, 2005; Joshi et al., 2016). In humans, changes in pupil size at constant luminance have long been used as a marker of central autonomic processes linked to cognition, including attentional effort (Hess and Polt, 1964; Kahneman and Beatty, 1966; Kahneman, 1973).

Therefore, we hypothesized that the operation of a behavioral goal with barely conscious awareness would influence the state of pupil-linked neuromodulatory systems, including the noradrenergic system via modulation of the dopaminergic system, resulting in more forceful voluntary motor action in the absence of conscious awareness. This prediction is in accord with several studies showing that noradrenergic neuronal responses are linked to effort-related motivation (Ventura et al., 2008, 2007; Bouret and Richmond, 2009; Bouret et al., 2012), and a previous report that the relationship between pupil dilation and increased mental effort in a digit retention task changed as a function of task difficulty after exposure to monetary rewards (Bijleveld et al., 2009).

Thus, in the present study, we investigated the influence of unconscious goal pursuit on the LC noradrenergic system state by examining pupil dilation with motivational rewards during the manipulation of barely visible goal-priming cues. Our results demonstrated that the barely conscious presence of a behavioral goal can influence the state of pupil-linked neuromodulatory systems, resulting in the production of more forceful voluntary motor actions, possibly via enhancement of dopaminergic system activity. To our knowledge, this study provides the first evidence that pupil dilation is related to implicit learning of the link between physical exertion and positive stimulus-induced reward signals during barely visible goal manipulation.

2. Materials and methods

2.1. Ethics statement

The experimental procedures complied with relevant laws and institutional guidelines, and were approved by the Human Research Ethics Committee of the Faculty of Sport Sciences, Waseda University (approval number 2014-272).

2.2. Participants and procedure

Sixty healthy right-handed (evaluated using the Edinburgh Handedness Inventory; Oldfield, 1971) Japanese participants took part in the study after providing both written and verbal informed consent (42 males, 18 females; mean age ± SD = 20.5 ± 1.6 years). Participants were university students at the Faculty of Sport Sciences, Waseda University, who engaged in regular physical exercise. Participants were assigned randomly to one of three groups (n = 20 for each group). Each group received two sets of tests consecutively (with at least a 15-min interval between sets). There were three conditions for each experimental (test) set: priming words related to physical exertion paired with subsequently displayed “reward” words (priming-plus-reward condition); priming words paired with non-reward words (priming condition); and no priming words (control condition). All three groups underwent a control condition to enable within-group comparisons. Thus, each group experienced the priming-plus-reward condition (priming-plus-reward group), priming condition (priming condition group), or the control condition (control groups), with four possible combinations. The number of participants for each possible order was as follows: (control, priming) 10; (priming, control) 10; (control, priming-plus-reward) 11; and (priming-plus-reward, control) 9. We used a between-subjects design to optimize the enhancement of the motor system (corticospinal excitability) via barely visible goal-priming with rewards (Takarada and Nozaki, 2014).

2.3. Priming procedure

To manipulate unconscious goal pursuit, we adopted an experimental procedure described in previous studies (Aarts et al., 2008; Takarada and Nozaki, 2014). Specifically, we used five Japanese words pertaining to the goal of physical exertion [“発揮する” (“exert”), “奮闘する” (“struggle”), “もがく” (“work hard”), “精を出す” (“energize”), and “努力する” (“strive”)], five positive adjectives [“素敵な” (“nice”), “素晴らしい” (“great”), “気分最高の” (“fantastic”), “満足な” (“satisfactory”), and “楽しい” (“enjoyable”)], and five neutral adverbs [“ほとんど” (“almost”), “少なくとも” (“at least”), “最終的に” (“finally”), “ほぼ” (“nearly”), and “すでに” (“already”)]. In the priming-plus-reward condition, for 25 of the 50 trials, barely visible presentation of one of the five exertion words was followed by fully visible presentation of one of the five positive words. For the remaining 25 trials, barely visible presentation of a random letter string was followed by fully visible presentation of one of the five neutral words. Therefore, the barely visible exertion primes were always paired with positive words. In the priming condition, the exertion primes were paired with neutral words (25 trials), and the random letter strings were paired with positive words (25 trials). This meant that although exertion primes and positive words were both displayed, they were never paired with each other. In the control condition, only random letter strings were used as primes and were paired with positive words on 25 trials and with neutral words on 25 trials; barely visible exertion words were never displayed. In this way, the viewing of positive and neutral words was balanced at 25 trials each, for all conditions. The order of possible stimuli pairs was randomized within each condition.

Each trial in each condition began with a 1000-ms presentation of five different strings of eight pseudorandom letters (DZXLTOTM, YSTZBXTU, VCFTHYPC, CBEXGTVY, and ZTAWYDBH) as a forward mask. This was followed by the barely visible prime, displayed for 33 ms. One randomly selected letter string among the original five was again displayed for 100 ms as a backward mask, after which a fully visible word was presented for 150 ms. Occasionally, a dot was presented for 33 ms (visible because of the absence of a backward mask), either above or below the neutral or positive word. Participants were instructed to indicate whether they had seen a dot, to bring the post-masked barely visible primes to their attention. Trials were carried out every 3.5 s within each condition. We used a 60 Hz CRT screen to display the words, and the experimental procedure was created with software designed for psychological experiments (Inquisit 3 Desktop Edition, Millisecond Software, Seattle, WA, USA).

In an independent test of the conscious perception of the primed exertion words, an additional sample of participants (15 males, five females; mean age S.D. = 21.4 ± 1.6 years, n = 20) underwent the priming-plus-reward conditions. In this test, participants were asked to indicate whether they saw a word related to physical exertion or not. The post-masked subliminal primes of exertion were attended to, but not reportable. The mean percentage of correct responses was 50.1 (SD = 6.6), indicating that their judgments were no different from chance, and they could not read the priming words.

2.4. Handgrip force measurement and subjective effort

Force was measured using a handgrip device (KFG-5-120-C*1-16*, Kyowa Electronic Instruments, Tokyo, Japan). After viewing all 50 stimulus pairs, participants were asked to squeeze the handgrip device with the right (dominant) hand when the word “squeeze” appeared on the display, and to stop squeezing when the word disappeared. The squeeze instruction was displayed for 5 s. The squeeze task was