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Neuropsychologia 45 (2007) 2387–2392

NEUROPSYCHOLOGIA

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Notes

Spontaneous eyeblink rate predicts the strength of visuomotor binding

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Received 14 September 2006; received in revised form 2 March 2007; accepted 2 March 2007
Available online 7 March 2007

Abstract

The primate cortex represents the external world in a distributed way, which requires for a mechanism that integrates the features of a processed event. Animal and patients studies suggest that feature binding in the visual cortex is under muscarinic-cholinergic control, whereas visuomotor integration is driven by the dopaminergic system. Consistent with this picture, we present evidence that the binding of visual and action features is modulated by spontaneous eyeblink rate (EBR), which is a functional marker of central dopaminergic function. Remarkably, the impact of EBR was restricted to the task-relevant visuomotor binding, suggesting that dopamine increased the maintenance of task-relevant information.

Keywords: Binding problem; Visuomotor integration; Neuronal synchronization; Dopamine; Spontaneous eyeblink

The so-called binding problem derives from the question of how our brain is able to properly integrate the feature codes that belong to a given event (Treisman, 1996). Candidates for solving such problem are conjunction detectors and neural synchronization. High-order cardinal cells (Barlow, 1972) are neurons onto which signals from neurons coding for the to-be-bound features converge. However, given the numerous ways in which discrete features can be potentially combined, the exclusive reliance on convergent mechanisms would lead to a combinatorial explosion and is therefore less plausible. The neural synchronization hypothesis (Engel & Singer, 2001), on the other hand, supposes that feature conjunctions are coded through the temporal coherence of the firing rates of cells referring to the same event. As compared to other mechanisms as conjunction detectors, synchronization would not only be a faster and more flexible mechanism but would also enable the representation of a very large number of novel and arbitrary feature combinations. Moreover, synchronization may mediate feature integration not only in perception but also in action planning and sensorimotor coordination, and other processes that require the binding of cortically distributed neural codes (Hommel, 2004). Indeed, evidence for a role of synchronization in feature integration has been found in visual perception (e.g., Keil, Muller, Ray, Gruber, & Elbert, 1999; for an overview, see Tallon-Baudry, Kreiter, & Bertrand, 1999) as well as in action planning (e.g., Pfurtscheller, Pregenzer, & Neuper, 1994; for an overview, see MacKay, 1997). In particular, action-contingent synchronization has been observed between motor and somatosensory areas of the monkey (Murthy & Fetz, 1992, 1996), and across the visual and parietal cortex and the parietal and the motor cortex of the cat (Roelfsema, Engel, Koenig, & Singer, 1997).

1. Neuromodulation of feature integration and eyeblink

In the recent years evidence has accumulated to suggest that at least two neurotransmitter systems are involved in feature integration and the creation of temporal coherence between cell populations: the muscarinic-cholinergic system, which seems to be linked to perceptual binding (Colzato, Erasmus, & Hommel, 2004; Colzato, Fagioli, Erasmus, & Hommel, 2005; Rodriguez, Kallenbach, Singer, & Munk, 2004), and the dopaminergic system, which seems to be responsible for the integration of action-related information (Schnitzler & Gross, 2005).

Dopamine seems to be involved in various premotor processes: Rihet, Possamaï, Micaleff-Roll, Blin, and Hasbroucq (2002) have demonstrated that L-dopa influenced stimulus processing in a choice reaction task, and Graybiel, Aosaki, Flaherty, and Kimura (1994) provided evidence for a role of dopamine in sensorimotor processing in conditional learning of stimulus–response parameters. Neuropsychological and neuro-

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0028-3932/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2007.03.004

physiological investigations (see for a review: Murray, Bussey, & Wise, 2000) have, in large part, identified the neural network that underlies the rapid acquisition and performance of arbitrary visuomotor mappings, which consists of parts of the premotor and prefrontal cortex, the hippocampal system, and the basal ganglia (BG). In particular, the BG, a main way station in the dopamine relay system, is known to play a substantial role in stimulus-behavior integration (Gurney, Prescott, & Redgrave, 2001). Consistent with this picture, Colzato, van Wouwe, and Hommel (2007) showed recently that the binding of visual and action features is modulated by the presentation of affect-inducing pictures, which can be assumed to stimulate the dopaminergic system. Preliminary results (Colzato & Hommel, submitted for publication) from our laboratory suggest also impairments in updating visuomotor binding among recreational users of ecstasy (MDMA) and cannabis, drugs that are notorious for impacting, among others, the dopaminergic system (Stone, Johnson, Hanson, & Gibb, 1988; Tanda, Loddo, & Di Chiara, 1999).

Interestingly, the functioning of the dopaminergic system seems to be reflected in the rate of spontaneous eyeblinks (EBR), which thus can be taken as a functional marker of central dopaminergic function (Blin, Masson, Azulay, Fondarai, & Serratrice, 1990; Kleven & Koek, 1996; Sax & Strakowski, 1998; Taylor et al., 1999). Schizophrenic patients, who have an increased activity of the dopamine system, show elevated blink rates (Freed, 1980), while blink rate is reduced in Parkinson's patients who suffer from a loss of nigrostratial dopaminergic cells (Deuschel & Goddemeier, 1998). Likewise, the blink rate is increased by administering dopaminergic agonists and decreased by dopaminergic antagonist (Lawrence & Redmond, 1991).

2. Purpose of study

Our study was motivated by the assumption that the integration of features across perception and action, but not in visual perception, is driven by the dopaminergic system (Schnitzler & Gross, 2005). Preliminary evidence for this assumption was provided by the success of our previous attempt to selectively target behavioral measures of visuomotor binding by presenting affect-inducing stimuli (Colzato et al., 2007). In the present study, we sought for converging evidence for the dopaminergic control of visuomotor integration by testing whether the strength of visuomotor binding can be predicted from spontaneous EBR, hence, an indicator of dopaminergic activity.

A second aim of our study was to determine under which circumstances dopamine modulates binding effects. Previous research (Hommel, 1998) showed that the strength of binding depends on the task-relevance of the respective feature dimension: stimulus features from task-relevant, and therefore attended dimensions affect later performance more strongly than features from task-irrelevant dimensions, suggesting that at least some aspects of the creation and/or the retrieval of bindings are under attentional control. Braver, Barch, and Cohen (1999) have suggested that dopamine is involved in increasing the maintenance of task-relevant information. If higher EBR indicates a higher level of dopaminergic depletion and if the latter is associated with focusing on task-relevant information, we would expect that the relationship between EBR and visuomotor integration is more pronounced with, or even restricted to the integration of task-relevant stimulus and response features.

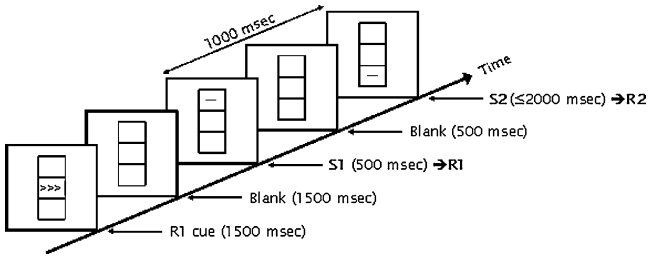

Fig. 1. Sequence of events in the present experiments (cf., Hommel, 1998). A response cue signaled a left or right key press (R1) that was to be delayed until presentation of S1, a red or green, vertical or horizontal line in a top or bottom box. S2 appeared 1 s later—another red or green, vertical or horizontal line in the top or bottom box. S2 shape signaled R2, also a speeded left or right key press. R2 speed and accuracy were analyzed as function of the repetition vs. alternation of stimulus shape, color and location, and of the response.

As behavioral marker for feature integration processes we adopted a variant of the task developed by Hommel (1998), which measures both visual–visual and visuomotor binding. In this task (see Fig. 1) participants are cued to prepare a left- or right-hand key press (R1), which they carry out as soon as S1 appears. The identity of S1 does not matter for the response but it varies in shape, location and color. One second later, S2 appears to signal R2, a binary-choice response to the shape of S2 (S2 color and location are entirely irrelevant to this version of the task). Performance in such a task reveals interesting interactions between repetition effects: it is impaired in partial-repetition trials, that is, if one stimulus feature or the response is repeated while the other is not (e.g., if shape repeats while location does not, or vice versa; or if shape repeats while the response does not, or vice versa). These *partial-repetition costs* suggest that the stimulus and response features of S1 and R1 are still bound when facing response features of R2, so that repeating a given feature (response location) will retrieve the event files the code of that feature has become a part of (Hommel, 1998, 2004). This creates conflict between the retrieved codes and those activated by the current response location of R2, thus delaying reaction time and increasing error rates. Crucial for our purposes is that these partial-repetition costs can be taken to indicate visual–visual (e.g., integration of shape and location stimulus feature) and visuomotor (e.g., integration of shape stimulus feature and response feature) binding. Note that in our version of the task, only shape was task-relevant, as subjects had to react whether the second stimulus was horizontal or vertical but could ignore its color and location.

In sum, we expected that EBR, as a functional marker of central dopaminergic function, would predict the strength of visuomotor binding (i.e., the size of the stimulus–response binding effect) in comparable way as affect does (Colzato et al., 2007). Moreover, given that dopamine is assumed to be involved in increasing the maintenance of task-relevant information (Braver et al., 1999), we speculated that EBR would

correlate with binding only for the task-relevant stimulus feature shape, that is, with the size of the shape–response binding effect.

3. Method

3.1. Participants

Eighteen young healthy adults served as subjects for partial fulfillment of course credit or a financial reward. Participants signed an informed consent form and were debriefed after the session. Furthermore, participants with a known history of drug abuse or psychopathology and those who were taking medication were excluded. All reported having normal or corrected-to-normal vision, and were not familiar with the purpose of the experiment. Three participants were excluded because it turned out that they did not comply with the instructions given by the experimental protocol.

3.2. Apparatus and stimuli

The experiment was controlled by a Targa Pentium III computer, attached to a Targa TM 1769-A 17″ monitor. Participants faced three gray square outlines, vertically arranged, as illustrated in Fig. 1. From viewing distance of about 60 cm, each of these frames measured 2.6° × 3.1°. A vertical line (0.1° × 0.6°) and a horizontal line (0.3° × 0.1°) served as S1 and S2 alternatives, which were presented in red or green in the top or bottom frame. Response cues were presented in the middle frame (see Fig. 1), with rows of three left- or right-pointing arrows indicating a left and right key press, respectively. Responses to S1 and to S2 were made by pressing the left or right shift-key of the computer keyboard with the corresponding index finger.

3.3. Procedure and design

The study consisted of two sessions (held in two different days) including, first, eyeblinks recordings and second, the actual experiment.

3.4. Eyeblink rate

Eyeblinks were recorded, with two horizontal (one left, one right) and two vertical (one upper, one lower) electrodes, for 6 min eyes-open segments under resting conditions. Given that spontaneous EBR is supposed to be stable during daytime but increases in the evening (8:30 p.m., as reported by Babarto et al., 2000), we never registered after 5 p.m. Additionally, we asked participants to avoid alcohol and nicotine consumption and to sleep sufficiently the day before the recording. Compliance with this instruction was motivated by announcing that saliva samples would be taken. As mentioned above, three participants were excluded because it turned out that they did not comply. Data were examined using the Brain Vision Analyzer (Brain Products™ GmbH, Munich, Germany; http://www.brainproducts.com/products/analyzer/index_analyzer.html). We defined an eyeblink as a voltage change of 100 μV in a time interval of 500 ms. Our sample of subjects had EBRs ranging from 3.7 to 13.3 per minute (S.D. = 2.8), which according to our assumptions should represent a wide range of tonic dopaminergic functioning.

3.5. Task

The actual experiment consisted of a 50 min session in which subjects completed a version of the task adopted from Hommel (1998) (see Fig. 1). Participants faced three gray, vertically arranged boxes in the middle of a monitor and carried out two responses per trial. R1 was a delayed simple reaction with the left or right key, as indicated by a 100% valid response cue (left- or

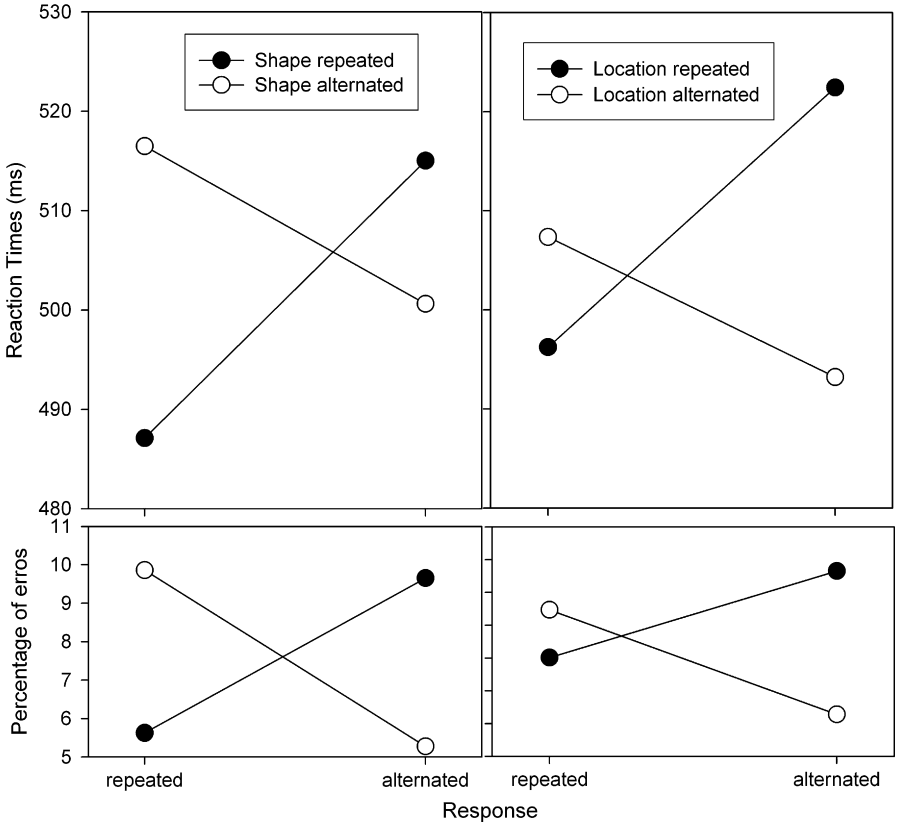

Fig. 2. Mean reaction times and error percentages for RT2 as a function of repetition vs. alternation of stimulus task-relevant feature and response. Typical binding effects are indicated by patterns showing worse performance for filled circle on the left and unfilled circle on the right (one stimulus feature is repeated while the response alternates, or vice versa).

Table 1
Results of analysis of variance on mean reaction time of correct responses (RT) and percentage of errors (PE)

Effect	d.f.	RT_{R2}		PE_{R2}	
		MSE	*F*	MSE	*F*
Color (C)	1.14	558.95	0.17	32.11	1.29
Location (L)	1.14	2087.29	2.29	31.03	4.11
Shape (S)	1.14	2144.57	1.61	54.69	0.01
Response (R)	1.14	3804.08	0.57	87.87	0.05
C × L	1.14	447.06	2.23	25.18	0.05
S × L	1.14	771.78	12.58**	30.72	0.76
S × C	1.14	601.72	0.32	58.73	0.97
S × L × C	1.14	711.60	0.20	16.90	0.00
C × R	1.14	560.72	0.10	30.52	3.42
L × R	1.14	490.84	49.72**	103.21	4.95*
S × R	1.14	1928.96	14.91**	35.10	31.68**
C × L × R	1.14	352.42	0.42	41.06	0.01
S × L × R	1.14	282.16	2.45	18.36	1.01
S × C × R	1.14	451.59	0.42	24.01	0.01
S × L × C × R	1.14	942.52	0.01	16.19	3.32

* $p < .05$.
** $p < .01$.

right-pointing arrow in the middle box) that preceded the trigger stimulus S1 by 3000 ms. S1 varied randomly in shape (a thin vertical or horizontal line), color (red or green), and location (top or bottom box). R1 was to be carried out as soon as S1 appeared, independent of its shape, color, or location; i.e., subjects were encouraged to respond to the mere onset of S1. R2 was a binary-choice reaction to the shape of S2 (vertical or horizontal), which also appeared in red or green, and in the top or bottom box, 1000 ms after S1 onset. Responses to S1 and to S2 were made by pressing the left or right shift-key of the computer keyboard with the corresponding index finger. Each session was composed of a factorial combination of the two possible shapes, colors and locations of S2, the repetition versus alternation of shape, color, location and the response, and three replications per condition ($2 \times 2 \times 2 \times 2 \times 2 \times 2 \times 2 \times 3 = 384$).

4. Results

After excluding trials with missing (>1500 ms) or anticipatory responses (<200 ms), mean reaction times (RTs) and proportions of errors for R2 were analyzed. ANOVAs were run with the repetition versus alternation of response (R1 → R2), stimulus shape, color and location (S1 → S2) as within-participant factors. Table 1 provides an overview of the ANOVA outcomes for RTs and PEs obtained for R2.

Replicating earlier findings (Hommel & Colzato, 2004), RTs revealed significant interactions between shape and location, $p = .003$, between response and shape, $p = .002$, and response and location, $p = .001$—repeating one but not the other feature slowed down responding (see Fig. 2).

The error rates followed the same pattern: response interacted with shape, $p = .001$ and location, $p = .043$. Both interactions were due to fewer errors in conditions where both features were repeated or both alternated, as compared to conditions where one feature but not the other was repeated.

After having replicated all theoretically relevant effects we computed Pearson correlation coefficients to indicate the relationships between the individually calculated spontaneous eyeblink rate and the sizes of binding effects[1] in visual perception (visual–visual binding) and across perception and action (visuomotor binding) for RTs and error rates (see Table 2). As

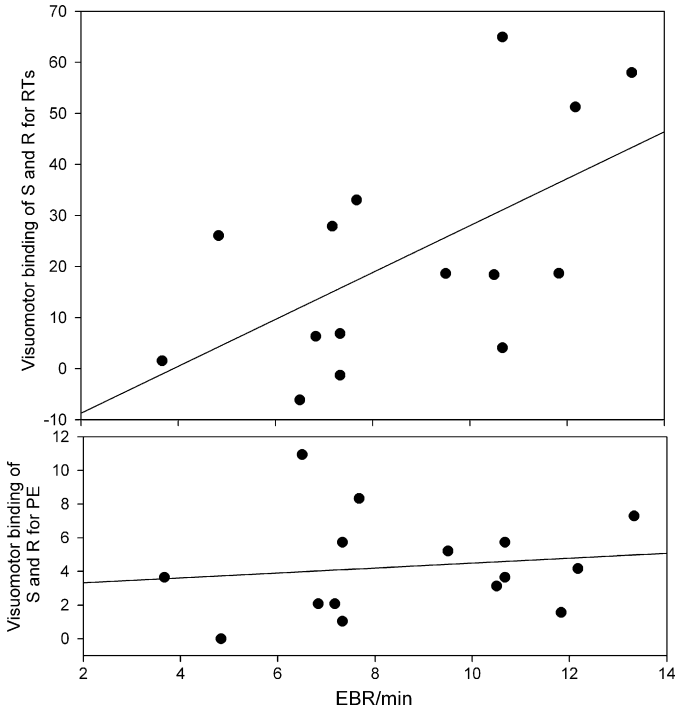

Fig. 3. Scatter diagram of individual spontaneous eyeblink rate (EBR) against the visuomotor binding effect of stimulus shape (S) and response (R) measured as stimulus (S1 − S2) repetition benefits for RTs and PE ($RT_{alternation} - RT_{repetition}$ and $PE_{alternation} - PE_{repetition}$) for stimulus shape as a function of response relation (R1–R2 repetition or alternation). $RT_{alternation}$ and $PE_{alternation}$ correspond to the mean of all conditions involving alternation of the respective stimulus feature (e.g., conditions Neither, L, C and LC, for stimulus shape) in the given response condition, while $RT_{repetition}$ and $PE_{repetition}$ correspond to the mean of all conditions involving repetition of that feature (e.g., conditions S, SL, SC and SLC).

Table 2
Correlations among individual score of spontaneous eyeblink rate (EBR) and the binding effects in visual perception (visual–visual binding) and across perception and action (visuomotor binding) for RTs and error rates (PE), in the first and second column, respectively

Type of binding		EBR/RT	EBR/PE
Visual–visual	Shape × location	$r = -.12$, $p = .67$	$r = .14$, $p = .31$
	Shape × color	$r = .07$, $p = .81$	$r = .07$, $p = .75$
	Color × location	$r = .34$, $p = .22$	$r = .23$, $p = .60$
Visuomotor	Shape × response	$r = .59$, $p = .021$	$r = .14$, $p = .62$
	Location × response	$r = .14$, $p = .61$	$r = .07$, $p = .79$
	Color × response	$r = .24$, $p = .39$	$r = .23$, $p = .60$

[1] Binding effects were calculated as the difference between the RTs for partial repetitions (feature X repeated and feature Y alternated, or vice versa) and the RTs for complete repetitions and "complete" alternations. That is, if features X and Y repeated and alternated, their binding effect B_{XY} would be $B_{XY} = (RT_{X/alt,Y/rep} + RT_{X/rep,Y/alt})/2 - (RT_{X/rep,Y/rep} + RT_{X/alt,Y/alt})/2$. Binding effects thus correspond to the 2-way interaction term of the respective features (and are thus immune to possible, but theoretically less relevant, main effects of feature repetition); a value close to zero means that the repetition effects of the two given features do not interact; a value greater than zero indicates a "binding-type" interaction of the sort described in the text.

expected, spontaneous EBR correlated (positively) only with the visuomotor binding effect of shape and response—hence, the correlation was restricted to the task-relevant stimulus feature. The correlation was positive in both RTs and error rates, but reliable in the former only. As Fig. 3 shows, partial-repetition costs of shape–response binding increased as function of increasing EBR.

5. Conclusions

Our findings show that the spontaneous EBR reliably predicts the strength of the binding between task-relevant stimulus features and the response. In contrast, EBR was unrelated to task-irrelevant visuomotor bindings and visual–visual bindings. Even though the correlative nature of our findings does not directly speak to the underlying causal relations, the observed pattern does fit with our previous demonstration that visuomotor binding is selectively enhanced through the presentation of pictures with positive valence (which are assumed to stimulate the dopaminergic system: Ashby, Isen, & Turken, 1999; Ashby, Valentin, & Turken, 2002). Taken together, these observations support the hypothesis that feature integration across perception and action is driven by the dopaminergic system—which possibly modulates neural synchronization (Schnitzler & Gross, 2005), while perceptual binding seems to be linked to the muscarinic-cholinergic system (Rodriguez et al., 2004).

Recent studies by Dreisbach et al. (2005) and Müller et al. (2007) provide evidence that higher spontaneous EBR facilitates the processing of novel stimuli—facilitating performance if a task switch requires attending to a novel stimulus and hampering it if the novel stimulus needs to be ignored. At first sight, this observation might be taken to conflict with the assumption of Braver et al. (1999) that dopamine (which presumably drives EBR) supports the maintenance of task goals, and it may seem inconsistent with our finding that EBR affects task-relevant features dimensions only. Given that our study employed a very different task, design, and rationale than those used by Dreisbach et al. (2005) and Müller et al. (2007), a direct comparison is difficult, especially if one considers that Dreisbach et al. and Müller et al. investigated the effects of (intentional) task-rule switches from one block to another, whereas we looked into (spontaneous) trial-by-trial effects with stimuli that did not differ in novelty. Nevertheless, one may speculate that differences in the sample were more crucial: Dreisbach, Müller and colleagues included a large proportion of subjects with very high blink rates, and thus ended up with much higher average rate (e.g., 18 blinks/min) in the Dreisbach et al. high group than we did (8 blinks/min). Interestingly, evidence suggests that the relation between dopamine level and cognitive performance follows an inverted U-shaped function, with best performance being associated with average dopamine levels (Goldman-Rakic, Muly, & Williams, 2000; Muly, Szigeti, & Goldman-Rakic, 1998). It may thus be that our sample is more representative of (and includes more) people with average dopamine levels whereas Dreisbach, Müller and colleagues investigated a group that was strongly biased to the upper, more extreme end of the function. Clearly, more systematic investigation of this issue is necessary, and we are currently addressing it in our laboratory.

Acknowledgments

We would like to thank Dr. Nachshon Meiran for suggesting the link between dopamine and eyeblink and Henk van Steenbergen for helping in the analyses of the eyeblink rate.

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