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## RESEARCH ARTICLE

# Pupil Diameter May Reflect Motor Control and Learning

Olivier White<sup>1</sup>, Robert M. French<sup>2</sup>

<sup>1</sup>Cognition, Actions et Plasticité, Sensorimotrice, INSERM UMR1093, Université Bourgogne Franche-Comté, Dijon, France.

<sup>2</sup>Laboratory for Research on Learning and Development (LEAD-CNRS), Université de Bourgogne Franche-Comté, Dijon, France.

**ABSTRACT.** Non-luminance-mediated changes in pupil diameter have been used since the first studies by Darwin in 1872 as indicators of clinical, cognitive, and arousal states. However, the relation between processes involved in motor control and changes in pupil diameter remains largely unknown. Twenty participants attempted to compensate random walks of a cursor with a computer mouse to restrain its trajectory within a target circle while the authors recorded their pupil diameters. Two conditions allowed the authors to experimentally manipulate the motor and cognitive components of the task. First, the step size of the cursor's random walk was either large or small leading to 2 task difficulties (difficult or easy). Second, they instructed participants to imagine controlling the cursor by moving the mouse, but without actually moving it (task modality: imagined movement or real movement condition). Task difficulty and modality allowed the authors to show that pupil diameters reflect processes involved in motor control and in the processing of feedback, respectively. Furthermore, the authors also demonstrate that motor learning can be quantified by pupil size. This noninvasive approach provides a promising method for investigating not only motor control, but also motor imagery, a research field of growing importance in sports and rehabilitation.

*Keywords:* cognition, motor control, motor learning, motor imagery, pupil diameter

One well-known function of the pupil is to regulate the flux of light entering the eye in response to changes in illumination through the so-called pupil light reflex. In addition, the relationship between pupil dilation and mental or emotional events has been studied for more than a century, starting with the work of Charles Darwin in 1872, who investigated the effect on pupil dilation of emotion and fear in humans and animals (Darwin, 1872).

Pupil size and pupil dilation have also been studied under increased cognitive load (Beatty, 1982; Hakerem & Sutton, 1966; Hess & Polt, 1964; Kahneman & Beatty, 1966), when anticipating a stimulus onset (Reinhard & Lachnit, 2002), or when experiencing sexual arousal (Hess & Polt, 1960), pain (Chapman, Oka, Bradshaw, Jacobson, & Donaldson, 1999), or habituation (White & Maltzman, 1978). It is widely documented that these mental events not only excite the sympathetic pupil dilator pathway but also inhibit the Edinger-Westphal nuclei, thus causing the relaxation of the sphincter muscle contributing to the dilation (Granholm & Steinhauer, 2004; Steinhauer, Siegle, Condray, & Pless, 2004).

Surprisingly, only a small number of studies have investigated the effect of physical activity on pupil dilation. However, to our knowledge, none specifically addressed

the link between pupil dilation and fine motor control. A seminal study by Simpson and Paivio in 1968 (Simpson & Paivio, 1968) showed that when participants were required to react to a stimulus with a key press (i.e., a motor output) there was greater pupil dilation compared to when an overt response was not required. More recently, participants pressed a button to provide a feedback about an ambiguous stimulus (Hupé, Lamirel, & Lorenceau, 2009). The authors found a correlation between pupil and motor responses. Furthermore, pupil diameters also increase with the perceived effort required to perform a power grip task at prescribed intensities (Zénon et al., 2014). Another recent study showed that physical activity itself increased pupil diameter in relation to the intensity of the activity (Hayashi, Someya, & Fukuba, 2010). The authors had participants perform incremental training on an ergometer while their pupils were monitored. Exercise has a large impact on autonomic control, and hence it was assumed it would increase the pupil diameter via sympathetic activation and/or parasympathetic withdrawal. In the above study, the decrease in the depth of focus was too small to have functional significance on acuity. The reasons for this pupil modulation during motor activity remains an open question.

Much of the cognitive system of the human brain has evolved in the service of motor control. Motor tasks, and especially those tasks involving fine motor control skills, invariably include significant premotor processes and high-level, cognitive, components. This is particularly true when beginning to learn a new task. The goal of our study is to characterize and understand the causal relationship between pupil diameter and processes involved in a fine motor task with two levels of difficulty. First, we verified that pupil diameter is indeed sensitive to motor preparation by comparing pupil dilation between the two task difficulties. Furthermore, in order to focus on non-motor-related effects only, we also assessed whether this distinction held in a motor imagery version of this same task (i.e., when participants imagined doing the task while making no actual movement). Second, we tested whether pupil dilation varied over time in an attempt to highlight motor learning effects. We hypothesized that (a) pupil diameter would be larger in

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*Correspondence address: Olivier White, Institut Marey, Université Bourgogne Franche-Comté, 64 rue de Sully, F-21000 Dijon, France e-mail: olivier.white@u-bourgogne.fr*

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the difficult task compared to the easy task, reflecting the more demanding premotor processes and (b) pupil dilation would decrease over time as participants learned the task.

## METHOD

### Participants

Twenty adult right-handed participants (10 women,  $M$  age = 21 years) from the Faculty of Psychology at the Université de Bourgogne (Dijon, France) gave written informed consent to participate in the study. All were informed that they could leave the experiment at any moment for whatever reason without incurring a penalty. They were naive to the purpose of the experiment, were familiar with the concept of motor imagery, and received course credit. All had normal or corrected-to-normal vision. This study was carried out in accordance with legal requirements and international norms (1964 Declaration of Helsinki), and approved by the Dijon Regional Ethics Committee.

### Experimental Procedures

The experiment was conducted in a quiet room. Each participant's right hand rested on a computer mouse with no buttons. We recorded pupil diameter at 120 Hz using a Tobii T120 eye tracker integrated into a 17-in TFT monitor (Tobii Technology, Stockholm, Sweden; refresh rate 50 Hz). Participants were seated at a distance of approximately 60 cm from the monitor. Visual stimulations and synchronization were controlled by a laptop running Mandriva Linux (Mandriva SA, France). The experiment was written using the Matlab Psychophysics Toolbox extensions (Version R2014b; The MathWorks, Natick, MA) and was connected to the eye tracker server through a local network. The laptop display controlled the experiment and the eye-tracker display was used as visual stimulation.

Before beginning the experimental session, gaze was calibrated for each participant. A sequence of 15 dots appeared sequentially on the screen for 3 s and participants were instructed to look at the targets. A linear regression was calculated to estimate the coefficients of the affine transformation from raw units to screen units (millimeters).

Each trial started with a 5-second interval during which a fixation white cross (in a 7.9-mm square, 1.3-mm-thick bars) and a blue circle (diameter 92.2 mm, 2.1 mm thick, 25 cd/m<sup>2</sup>) appeared at the center of the screen (black background, 4 cd/m<sup>2</sup>). The fixation cross was then replaced with a yellow circular cursor (diameter 4 mm) that started to move on the screen following a random walk for 25 s. The (x,y) cursor position was generated by  $\begin{bmatrix} x \\ y \end{bmatrix}_{t+1} = \begin{bmatrix} x \\ y \end{bmatrix}_t + \begin{bmatrix} \theta_x \\ \theta_y \end{bmatrix}$ , with  $\theta_x, \theta_y \sim N(0, \sigma)$ . Within each session, 10 trials were easy and 10 trials were difficult. In the easy condition, the cursor random walk was generated with

$\sigma = 10$  pixels and smoothed by a Gaussian filter (kernel width = 10 mm). In the difficult condition, we set  $\sigma = 35$  pixels and the kernel width to 4 mm. In other words, the cursor moved much more quickly and rapidly in the difficult condition than in the easy condition. We ensured that the cursor never went outside the screen boundaries. Furthermore, all time series were calibrated such that the cursor spent on average 20% of its time within the blue circle. An algorithm generated these series offline and saved them to files.

The experiment consisted of two sessions of 20 trials each and lasted about 30 min. The real movement session was always followed by the imagined movement session. In the real movement condition, participants used the computer mouse to control the movement of the cursor in order to attempt to confine it to the circle (mouse to screen gain: 1.5 in X and Y dimensions). Mouse positions ( $M_x, M_y$ ) were added to the random walk of the cursor before the resulting position ( $C_x, C_y$ ) was displayed on the screen:  $\begin{bmatrix} C_x \\ C_y \end{bmatrix} = \begin{bmatrix} x \\ y \end{bmatrix} + \begin{bmatrix} M_x \\ M_y \end{bmatrix}$ . If participants could perfectly anticipate the trajectory of the cursor, they would be able to perform compensatory mouse movements such that  $t_{C_y}^C = t_0^0$ . However, the random nature of the task prevented them from doing so. In the imagined movement session, participants rested their hand on the mouse but were instructed not to move the mouse. Instead, they had to imagine what motor commands would be necessary to keep the cursor in the circle without actually executing them. The exact instruction in French was, "*Imagine-toi exécuter le mouvement de la même manière que si tu le faisais réellement, en ressentant les sensations d'un vrai mouvement, mais sans contracter les muscles. Tu dois te sentir faire le mouvement en étant à l'intérieur de ton corps et non en te voyant de l'extérieur*" (Imagine moving the cursor exactly as you would really move it and imagine the associated feelings, without contracting your muscles. You should feel yourself doing the movement from the inside, rather than having the sensation of watching yourself from the outside). In each session, participants were tested on 10 easy trials and 10 difficult trials that were randomly interleaved and not cued.

## DATA ANALYSIS

### Performance Index

During each trial, participants attempted to keep the cursor in the central circle as long as possible. We recorded the cursor position and a performance index was defined as the proportion of time the cursor spent in the circle. Each trial was calibrated so that the performance index without intervention of the participant would be between 18.5% and 21.5%.

## Extraction of Normalized Pupil Diameters

Raw pupil diameters of individual subject's eyes were preprocessed for each trial. First, we verified that the time series for the pupil diameters of both eyes were correlated ( $r = .99, p < .001$ ), which allowed us to pool the data from both eyes. We then calculated a baseline,  $b$ , as the mean pupil diameter during the first 3 s. Normalized time series  $N(t)$  were calculated from raw time series  $R(t)$  according to  $N(t) = 100 \left( 1 + \frac{R(t) - b}{R(t)} \right)$ . Variations are expressed in % relative to baseline  $b$  (100%). We also computed a linear regression  $\alpha N(t) + \beta$  through the last 18 s of averaged pupil dilations in each trial. We used statistical tests on offsets ( $\beta$ ) of the regression to quantify differences between normalized pupil diameters time series. This provides a more robust comparison of normalized pupil diameters between conditions as the regression parameters are calculated for all samples of the time series.

## Analysis of Saccades

Two dimensional gaze movements were differentiated twice and we used a  $750^\circ/s^2$  acceleration threshold to detect saccades during each 30-second trial (see de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002). Then, we calculated the angular direction of each saccade ( $dir_S$ ) and the angular direction from gaze position at saccade onset to the center of the circle ( $dir_C$ ). We then classified saccades in two groups. Centripetal (CP) saccades tended to move toward the center of the circle ( $|dir_C - dir_S| \leq 90^\circ$ ) while centrifugal saccades ( $90^\circ < |dir_C - dir_S| \leq 180^\circ$ ) tended to escape from the circle.

# RESULTS

## Performance and Eye Movement Data

Figure 1 quantifies the performance of participants when they attempted to keep the cursor in the circle. In the easy condition, participants reached a maximal performance of 100% from the outset (Figure 1A, red series). However, participants only reached 71.6% in the difficult condition (easy vs. difficult,  $F(1, 19) = 2478.1, p < .001, \eta_p^2 = .99$ ). Participants scores did not improve across trials, main effect of trials,  $F(9, 171) = 1.4, p = .197$ ; and there was no interaction between modalities,  $F(9, 171) = 1.3, p = .229$ . The unpredictability of the task made it impossible to develop strategies to improve in the difficult condition.

Humans track moving objects with a combination of saccadic and smooth-pursuit eye movements. Random behavior, as in the present paradigm, eliminates an individual's ability to accurately predict target motion. Therefore, catch-up saccades are unavoidable when the movement of the cursor is fast and varies randomly in direction. We quantified the difference between saccadic and smooth-pursuit eye movements by calculating the

cumulated distance covered by the gaze during a trial. We found that gaze traveled the same screen distance in both easy and difficult tracking conditions (Figure 1B;  $M = 1110$  mm,  $SD = 756$  mm),  $t(19) = .17, p = .864$ .

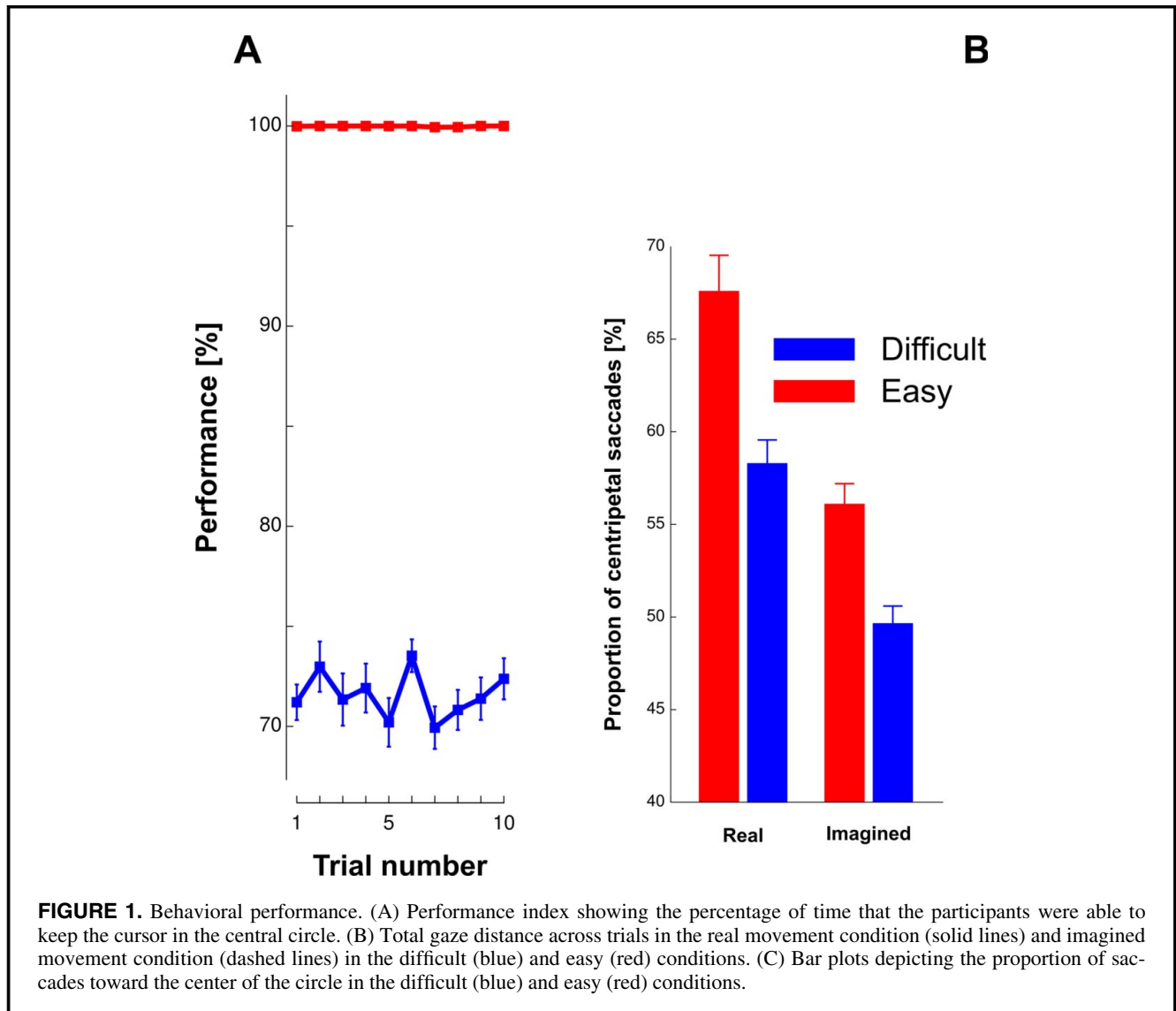
In the imagined movement condition, with no interaction between hand and mouse, gaze was still active. Namely, it covered a cumulated mean distance of 2459 mm ( $SD = 1026$  mm; i.e., combining the easy and difficult task conditions), significantly more than in the real movement condition,  $t(19) = -8.8, p < .001, \eta_p^2 = .8$ . A three-way repeated measures analysis of variance (ANOVA) confirmed this result by reporting main effects of task,  $F(1, 19) = 25.7, p < .001, \eta_p^2 = .57$ ; and movement type,  $F(1, 19) = 69.8, p < .001, \eta_p^2 = .79$ ; but no trial effect,  $F(9, 171) = .9, p = .544$ . Interestingly, in the imagined movement condition, a paired  $t$  test showed that gaze was more active in the difficult condition than in the easy condition,  $t(19) = -7, p < .001, \eta_p^2 = .72$ . Accordingly, we found that participants triggered more saccades in the imagined movement condition than in the real movement condition (512 vs. 243),  $t(19) = 6.1, p < .001, \eta_p^2 = .66$ .

The previous analysis does not provide much detail about direction of saccades in the different conditions. Therefore, we went one step further and analyzed the direction of saccades with respect to the target circle. Figure 1C depicts the proportion of CP saccades (eye movements made toward the circle) in the two modalities and task difficulties. Saccades were mostly CP (overall  $M = 57.9\%$ ,  $SD = 8.9\%$ ; significantly  $>50\%$ ),  $t(79) = 7.9, p < .001, \eta_p^2 = .44$ . Furthermore, a two-way ANOVA highlighted a main effect of movement type,  $F(1, 76) = 32.2, p < .001, \eta_p^2 = .2$ ; and task difficulty,  $F(1, 76) = 53, p < .001, \eta_p^2 = .33$ ; but no interaction,  $F(1, 76) = 1, p = .311$ ;  $t$  tests revealed that there were more CP saccades in the easy than difficult condition,  $t(19) = 10.9, p < .001, \eta_p^2 = .89$ , and in the real movement than imagined movement condition,  $t(19) = 5.3, p < .001, \eta_p^2 = .6$ .

In sum, performance saturated at maximum in the easy condition and reached a plateau in the difficult condition, from the very first trial. Gaze was more saccadic during the imagined movement condition than during the real movement condition and presented more CP saccades.

## Pupil Diameter is Modulated by the Difficulty of a Motor Task

Figure 2A depicts averaged normalized pupil diameters as a function of time in the easy (red trace) and difficult conditions (blue trace). We analyzed pupil diameter data between 5 s after cursor onset throughout the end of the trial. A two-way repeated measures ANOVA revealed significant main effects of task,  $F(1, 19) = 72.32, p < .001, \eta_p^2 = .79$ ; and movement type,  $F(1, 19) = 14.92, p = .001, \eta_p^2 = .44$ . The interaction was also significant,  $F(1, 19) = 13.82, p = .002, \eta_p^2 = .42$ . A two-tailed paired  $t$  test revealed



that pupil dilation in the difficult condition was larger than in the easy condition for both real,  $t(19) = -8.22, p < .001$ ; and imagined movement modalities,  $t(19) = -5.51, p < .001$  (Figures 2A and 2B). These results clearly demonstrate that pupil diameter increases with task difficulty.

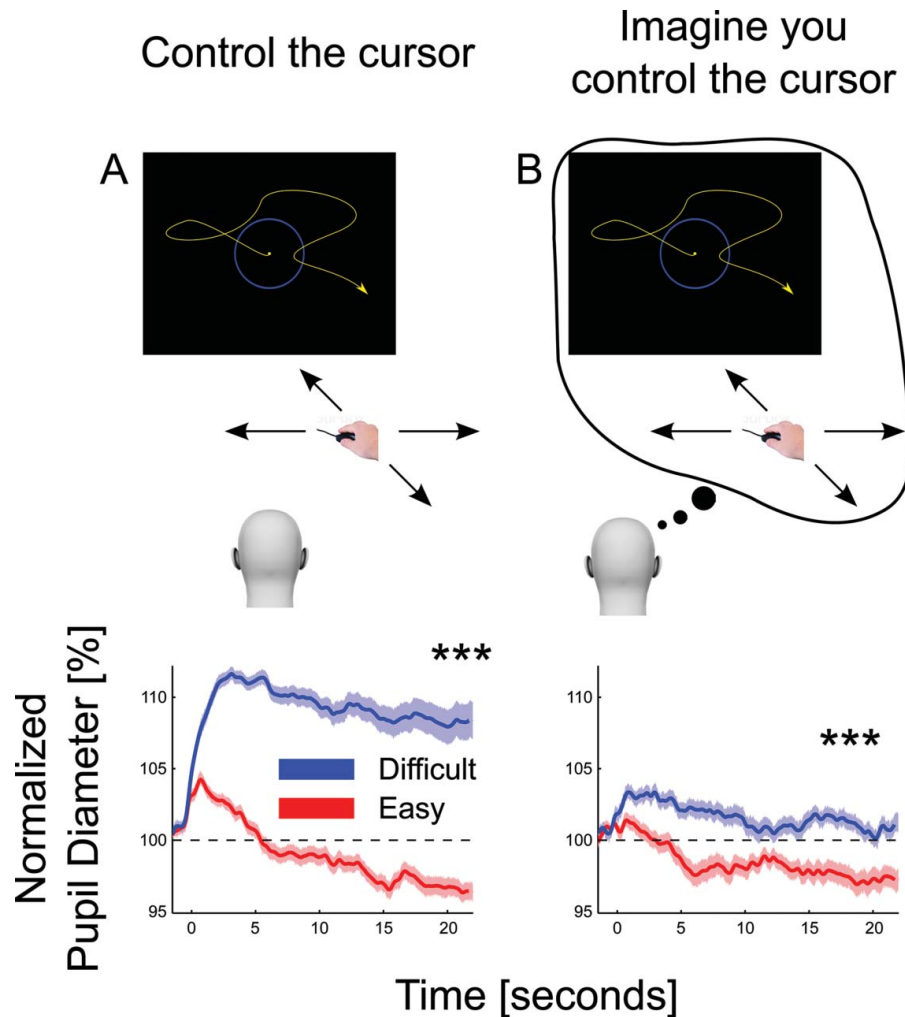
Real and imagined movements share similar brain areas and cortical processes (Ehrsson, Geyer, & Naito, 2003; Gerardin et al., 2000; Macuga & Frey, 2012; Nair, Purcott, Fuchs, Steinberg, & Kelso, 2003; Sirigu et al., 1996). However, there are differences between the real movement and imagined movement conditions. First, it is possible to see the imagined task as a truncated version of the real task, as motor output is voluntarily inhibited in the former. Second, although sensory inflows still exist in the imagined movement condition, this feedback is voluntarily not processed by the central nervous system. Nonetheless, one can still see significant differences in pupil dilation between both

task difficulties when participants only imagined performing the task (Figure 2B).

### Pupil Diameter is a Reliable Indicator of Trial-by-Trial Learning

Participants' performance failed to improve over time. We did not find any evidence of a progressive change of strategy in controlling the mouse or in coordinating their gaze over trials. However, pupil diameter decreased over time within a trial. We now ask whether pupil diameter may also show some change across trials.

Figure 3 plots 10 normalized pupil diameters in the easy (left panel) and difficult conditions (right panel) over time and averaged across participants. Blue colors correspond to earlier trials (color gradient from blue to



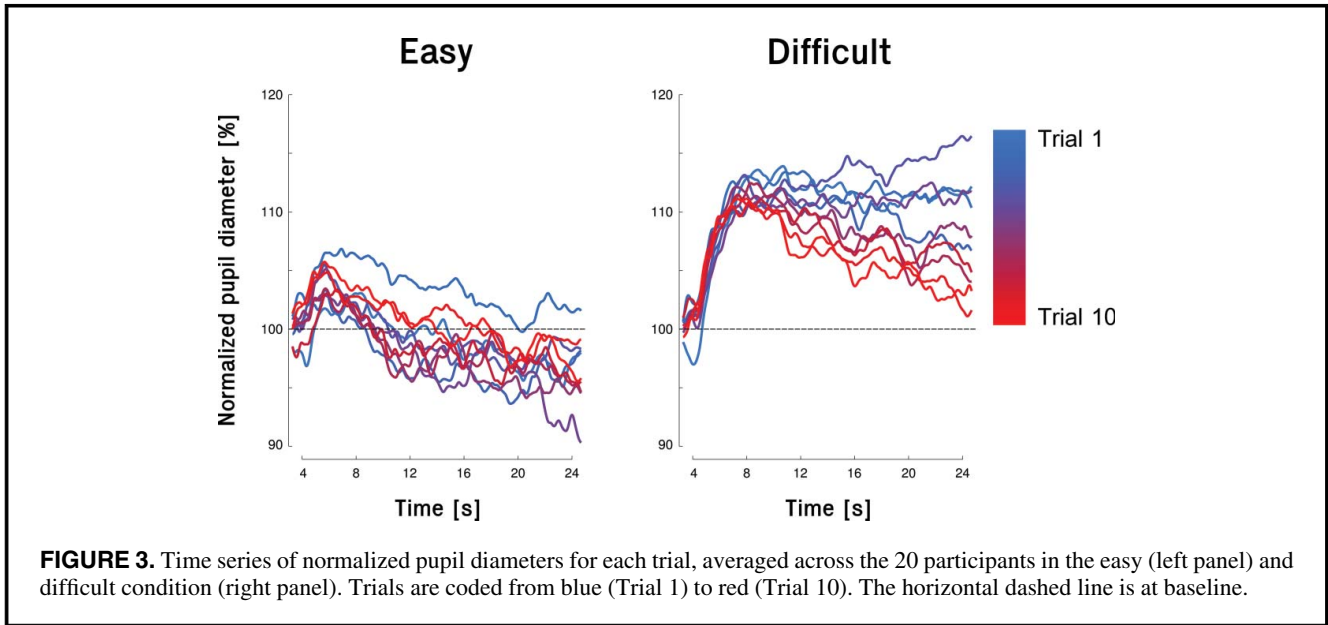
**FIGURE 2.** Experimental design and time series of pupil diameters. (A) Participants (20) controlled a yellow cursor with the computer mouse. Normalized pupil diameters (y-axis) over time (x-axis) were larger in the difficult condition (blue trace) than in the easy condition (red trace). Time 0 corresponds to cursor onset. (B) The same participants imagined the motor commands required to maintain the cursor in the circle without actually moving the mouse. The difficult condition again induced the largest pupil diameters. \*\*\*Statistical significance at  $p < .001$ .

red, Trials 1–10). In the easy condition, individual trials overlap (Figure 3, left panel). In contrast, the pattern is different in the difficult condition (Figure 3, right panel). First, time series overlap up to around 6 s after the cursor appeared. Then trials diverge in a fan-like manner: Early trials show monotonic increase in pupil diameters, whereas late trials show a decrease over time. This pattern explains the larger errors at the end of the averaged trial (Figure 2A, difficult). To better characterize this effect, we extracted mean pupil diameters during the last 5 s in the four conditions (two tasks by two movement types). We then calculated their correlation with trial number. Figure 4 shows that this trial ordering holds only in the real movement and difficult condition (Figure 4, left panel, blue;  $r = -.78$ ,  $p = .008$ ) and not the other (all  $|r| \leq .43$ ,  $p > .219$ ).

Overall, we showed that in the absence of explicit change in behavioral performance, pupil diameter decreased over two time scales. First, after a stereotyped increase, it then constricted as time elapsed (seconds). Then, despite easy and difficult trials being randomly intermixed, over the course of successive trials, pupil diameters decreased in the difficult condition (minutes).

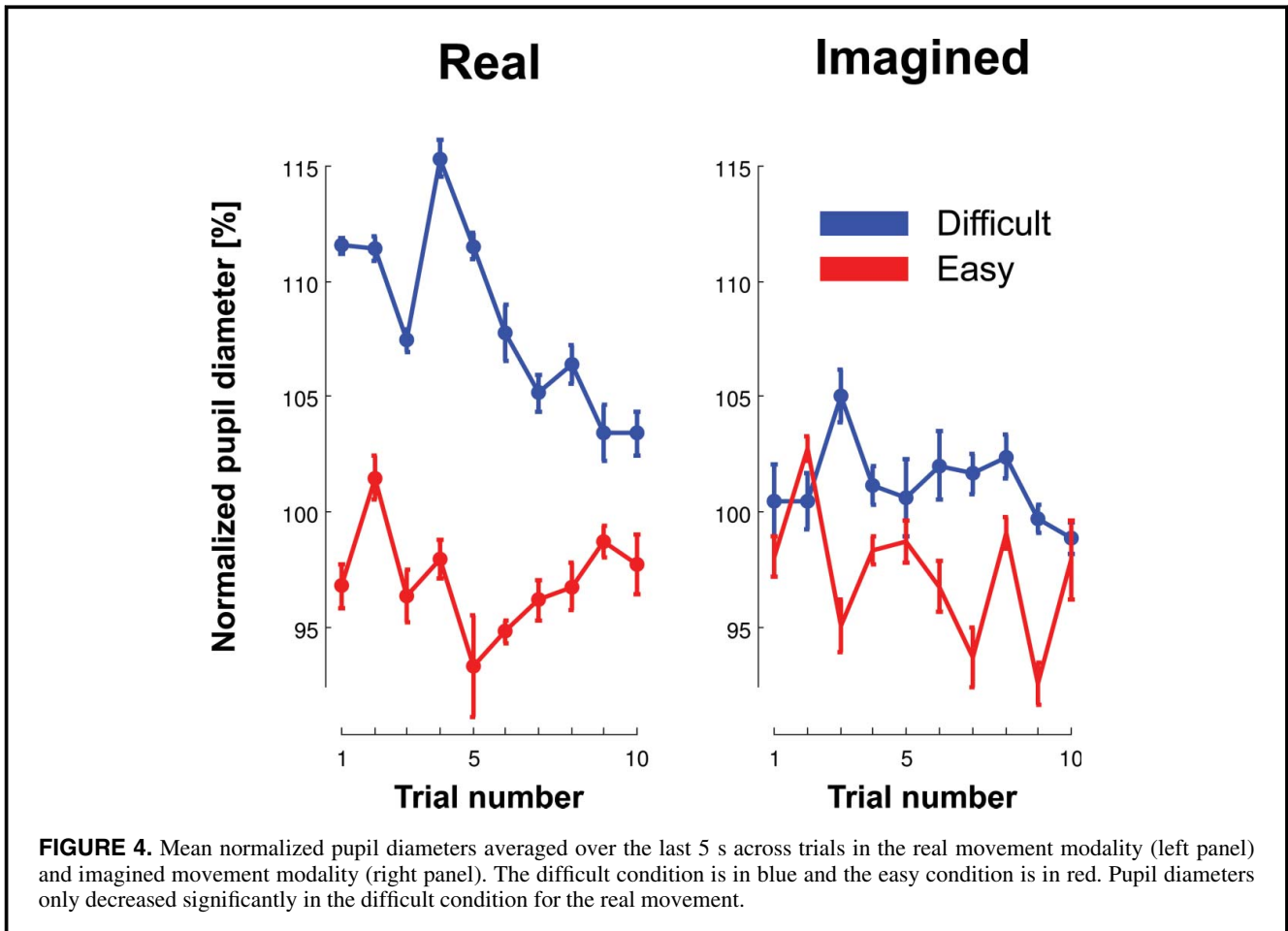
## DISCUSSION

Participants used a computer mouse to control the random trajectory of a cursor moving on a computer screen. The cursor was programmed to move with either high (difficult) or low (easy) degree of variability. In a first condition, participants moved the mouse in such a way as to keep the randomly moving cursor in a central circle on the



screen. In a second condition, participants only imagined the movements they would have made in order to maintain the cursor in the central circle. The two main results of

these experiments confirmed our predictions and were the following. First, pupil dilation was larger for the difficult compared with the easy condition both in the real



movement and imagined movement modalities. Second, pupil diameters notably decreased within and across trials, especially in the more challenging difficult conditions. These two results are now discussed.

### **Pupil Dilation Reflects Premotor Processes**

While it has long been known that pupil dilation is related to arousal (Beatty, 1982), only a few studies showed that pupil responses are, to various extents, also correlated with motor activity (Hayashi et al., 2010; Hupé et al., 2009; Simpson, 1969). Our data are in broad agreement with most of these studies, although they lead to new interpretations. An earlier result by Simpson in 1969 (Simpson, 1969) showed larger pupil dilation for participants who had to press a key to fulfill a pitch discrimination task. In a second, more recent study, participants had to provide feedback about an ambiguous stimulus with a button press (Hupé et al., 2009). The authors showed that 70% of the observed pupil dilation could be accounted for by the decision and motor components. In a third study, pupil sizes of participants training on an ergometer also increased (Hayashi et al., 2010). However, pedaling is a rhythmic activity requiring little movement planning (Schaal, Sternad, Osu, & Kawato, 2004). In addition, the muscular effort involved in pedaling is much greater than that required by skilled and dexterous manipulations. Therefore, pupil size could have increased via sympathetic activation or parasympathetic withdrawal.

In most previous studies investigating the effect of motor activity on pupil size, the cognitive component has not been controlled for with any degree of accuracy. In the work presented here we were able to manipulate cognitive load in two ways. First, we contrasted pupil diameters between two levels of difficulty of the same task. When debriefed, participants reported that it was nearly effortless to maintain the cursor within the circle in the easy condition whereas they only reached 72% in the difficult condition. The task goal could be achieved by minimizing an error signal dependent on the position of the cursor and the target circle. This error-based control strategy clearly necessitated some mental effort. Indeed, this motor action required complex and continuous updating of state variables, such as hand position, velocity or force involving an appropriate internal model (Kawato, 1999). The position of the cursor had to be processed visually in real time and, depending on its current position and velocity, a prediction of its trajectory had to be computed to adequately alter the trajectory with the mouse. We hypothesized that the increased pupil dilation observed in the difficult condition would reflect the additional workload of processes implemented in brain areas such as the posterior parietal cortex, the supplementary motor area, and the premotor cortex (Desmurget & Sirigu, 2009).

Second, we also compared pupil dilations between two different modalities, imagined and real, of the same task.

Undoubtedly, mental load is increased in both modalities because similar premotor processes were engaged in the real movement and in the imagined movement conditions (Ehrsson et al., 2003; Gerardin et al., 2000; Macuga & Frey, 2012; Nair et al., 2003; Sirigu et al., 1996). We found larger pupil dilation in the real movement condition compared to the imagined movement condition. This finding is in agreement with a recent and elegant study that demonstrated that pupil size reflected the level of effort invested in a task, irrespective of whether it is physical or mental (Zénon et al., 2014). The main difference between motor imagery and actual movements is the inclusion of the outer loop (real feedback) in the latter case. Therefore, this suggests that the difference between pupil dilation observed in the real and imagery movement conditions reflects the workload necessary to process feedback in the real motor task.

It is worth reporting that, even in the imagined movement condition, some motor output was present: participants performed more saccades in that modality. It could therefore be argued that pupil dilation could be driven, at least in part, by oculomotor activity. However, this was not the case, as the cumulated distance covered by the saccades was not proportional to pupil dilation (Figures 1B, 2A, and 2B). We found different patterns of eye movements between the real movement and imagined movement conditions. Usually, eye movements during motor imagery are similar to those that occur during the corresponding real movement (Laeng, Bloem, D'Ascenzo, & Tommasi, 2014; Laeng & Sulutvedt, 2014; Mast & Kosslyn, 2002). However, most previous experiments that investigated eye movements in imaginary tasks involved only very simple static stimuli, such as geometric shapes. Our imaginary task was not static and involved controlling a partially uncontrollable cursor, which was far more complex than viewing a static image. In contrast, the eye movements in the real movement condition were necessary to maintain the cursor in the circle. This meant that the variability of the random walk could have been partially compensated for, leading to smaller subsequent saccades. However, in the imagined movement condition, if the oculomotor strategy was the same as in the real movement condition, no partial compensation was possible (as the participants were not, in fact, controlling the position of the cursor), and, therefore, longer CP saccades occurred. Significantly, the large proportion of saccades toward the circle in the imagined movement condition is a good indicator that participants are actually attempting to do the task in this condition.

### **Pupil Diameter is Sensitive to Motor Learning**

The human brain has a remarkable ability to learn complex motor skills. When confronted with a task for the first time, an exploratory yet cognitively expensive behavior guides our movement. Then, feedback provides information about how well the movement has been executed. These



signals will, in turn, allow us to tune our internal model and be more successful in subsequent trials.

In many contexts, learning is synonymous with improvement of performance, such as a faster pace, increased accuracy or better coordination. Motor-skill learning can be accompanied by both increases and decreases in brain activity. Increases may indicate neural recruitment, while decreases may imply that a region has become unimportant or developed a more efficient representation of the skill. Learning processes are sometimes referred to as habituation or automaticity as they refer to the reduction of the mental effort required to perform a task (Schneider & Shiffrin, 1977). Habituation involves decreased sensitivity or response strength with repeated stimulus presentations (Privitera, Renninger, Carney, Klein, & Aguilar, 2010), all the while keeping performance at a good stable level. Repetition suppression paradigms in functional magnetic resonance imaging are based on these principles. A recent study showed that some brain areas activate less and less as a subject learns a new task. In other words, as one becomes expert, the network engaged in the task becomes more efficient, and therefore less activated (Wiestler & Diedrichsen, 2013). The authors found consistently decreased activation on parietal areas with sequence training. This is further supported by studies involving musicians that have shown decreased activity at least in secondary motor areas (Hund-Georgiadis & Von Cramon, 1999).

Our data are in agreement with this work on habituation. In the difficult trials, pupil diameters of participants initially increased. However, over time, pupil size decreased between trials, but also within individual trials, even though performance remained constant. We speculate that pupil diameter indirectly reflects brain activity specifically engaged in learning a motor task. In support of this hypothesis, it was shown that the activity of locus coeruleus neurons appears in the earliest stages of learning, usually before corresponding changes can be noticed in frontal areas (Bouret & Sara, 2004). To our knowledge, this is the first time a truly noninvasive method, requiring no physical contact with the participant, quantifies the degree of fine motor learning.

## CONCLUSION

The present study makes a clear causal and descriptive link between pupillometry and fine motor control. By manipulating the cognitive demands of the tasks, we showed that pupil diameters reflect neural processes involved in motor preparation and in the processing of feedback. Furthermore, we also demonstrate that subtle aspects of motor learning can be quantified by pupil size, on a trial basis. This noninvasive approach can therefore quantitatively complement current methods based on comparatively inaccurate measurements such as chronometry and self-reporting questionnaires and provide a promising method for investigating not only motor adaptation but also motor imagery, a research field of growing importance in rehabilitation.

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