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Gaze and the Eye Pupil Adjust to Imagined Size and Distance

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Abstract

Pupillary responses and associated vergence eye movements were monitored during imagery of objects of differing sizes ("large" or "small") from varying distances ("near" or "far"). Objects' imagined size and distance affected oculomotor behavior. Objects visualized as "far" resulted in the larger pupil dilations and smaller visual angle, while small objects imagined "near" were associated with smaller pupils in contrast to relatively larger pupils when imagined as "far" away. Furthermore, near objects resulted in larger visual angle, and particularly, vergence adjustments were observed that were dependent on imagined size and distance of the small objects. The findings are consistent with the idea that imagery emulates perception, also at the embodied level of oculomotor behaviors.

Keywords: Imagery; Pupillometry; Vergence; Object size; Distance; Embodied cognition

1. Introduction

According to an influential theory of mental imagery, when visualizing objects or scenes, the brain emulates perception (Moulton & Kosslyn, 2009) by reconstructing brain states in the cortex's visual and motor areas, similar to those occurring in comparable perceptual events (for reviews, see Ganis, Thompson, & Kosslyn, 2004; Pearson, Naselaris, Holmes, & Kosslyn, 2015). Embodied aspects of cognition also play a role in visual imagery, since it has been found to be affected by body position (Mast, Ganis, Christie, & Kosslyn, 2003) and to rely on motor representations (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Jeannerod, 1994; Laeng, Bloem, D'Ascenzo, & Tommasi, 2014; de'Sperati, 2003; Wexler, Kosslyn, & Berthoz, 1998), as well as being capable of influencing the perception of motion and self-motion (Nigmatullina et al., 2015; Winawer,

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Huk, & Boroditsky, 2010). According to Moulton and Kosslyn (2009), a key purpose of imagery is to make predictions and answer "what if" questions about potential consequences through mental simulation of specific actions or scenarios. Although we may not encounter the imagined scenarios in perception, it seems vital that mental images can simulate perceptual properties, in order to be appropriate models of the real world. Since imagery emulates perception and influences what we perceive in a given situation, it would be optimal if the low-level sensory features would be re-represented in the mental image (Rouw, Kosslyn, & Hamel, 1997) so as to be best prepared for possible scenarios (Pearson et al., 2015). Hence, both the distance and size of an imagined object should be simulated during the imagery process, since these aspects are essential elements in typical visual experience.

In perception, people are able to competently judge both perceived size and distance under normal conditions (i.e., standing/sitting upright; e.g., Higashiyama & Adachi, 2006). There is also empirical support for the claim that spatial properties are embodied in images. A series of clever experiments by Kosslyn (1978) investigated the visual angle at which images appeared to "overflow" when participants imagined moving toward objects with their eyes closed, and they found that the distance at which imagined objects "overflowed" varied with the size of the objects, just as seen during perception of comparable objects.

Similarly, Ruggieri and Alfieri (1992) measured the accommodation of the crystalline lens through an ecographic system, while the participants imagined near stimuli, that is, reading phrases from a book, or far stimuli, like seeing a ship on the horizon. The near and far imagined stimuli modified the bending radius of the crystalline lens, thus producing a physiological accommodation similar to that of visual perception for near and far objects. These findings are consistent with the view that imagery emulates perception and involves bodily adjustments of the oculomotor system. Importantly, this study only measured the crystalline lens' accommodation to one very near stimulus and one stimulus perceived very far away.

In this study, we reasoned that if a key role of imagery is to aid behavioral decisions through predictions of the various potential outcomes of situations (Moulton & Kosslyn, 2009), imagery of objects of varying size at several different distances should emulate perception by also adjusting pupil size and eye vergence to the imagined situation. Indeed, several aspect of the oculomotor response to objects' size and distance should be involved during imagery's emulation of perception. Eye-tracking studies have confirmed that the oculomotor system is remarkably active during mental imagery, as in guiding eye gaze (Brandt & Stark, 1997; Laeng & Teodorescu, 2002; Laeng et al., 2014; Martarelli, Chiquet, Laeng, & Mast, 2016). Other aspects of ocular control like adjustments of the crystalline lens (Ruggieri & Alfieri, 1992) and of the diameters of the eye pupils occur during visual imagery and, crucially, in a similar manner to viewing the luminance of actual objects or scenes in perception (e.g., Laeng & Sulutvedt, 2014); that is, pupils dilate when just thinking about "dark" objects or events and constrict in response to "bright" scenes, while the observers are actually looking at an unchanging, empty screen. Similar pupillary adjustments have been reported to occur when reading words naming

dark/bright objects (Mathot, Grainger, & Strijkers, 2017), also suggesting that mental images may be generated spontaneously during reading.

However, to our knowledge, no study has investigated whether *pupil diameter* and *vergence*, that is, two of the key elements in the so-called pupillary near response (PNR) during perception, would also be enacted when imagining differently sized objects at various distances. Positive evidence for the occurrence of an imagery-related PNR and/or vergence response would further support the idea that aspects of imagery are embodied in action (Hebb, 1968) and that these bodily adjustments may optimize its emulation of perceptual processes (Laeng & Sulutvedt, 2014; Laeng & Teodorescu, 2002; Pearson et al., 2015) and the view that imagery and perception share overlapping processes (Kosslyn, 1978, 1994).

In addition to pupil dilation and constriction, a fundamental component of the pupillary response expressed when looking at specific objects is the vergent eye movements onto objects (Fincham & Walton, 1957). That is, our eyes rotate so that the projection of an object is centered in the retinae in both eyes. When looking at an object close by, the eyes rotate toward each other (convergence), and, in contrast, for an object farther away they rotate away from each other (divergence). The net effect of these adjustments of gaze direction is that both pupils converge onto a singular point in space to facilitate focus on near objects, or alternatively diverge to facilitate focus on objects at a far distance. By constricting, the pupil increases the depth of focus of the eye, blocking the light scattered by the periphery of the cornea, and reducing defocus across the depth planes (Jampel, 1972). At the same time the eye lens should increase its curvature to become more biconvex so as to increase refractive power and, typically, when focusing overt attention on objects positioned at different distances, vergence and accommodation adjust together, a phenomenon also known as the accommodation-convergence reflex. However, this accommodation response is not captured by infrared eye-tracking systems, as the one used in this study; hence, we will focus on documenting the existence of imagery-related changes in pupil diameter and in proximal vergence (i.e., changes in the eyes' angle of convergence when "virtually fixating" onto an object imagined near or far, in the absence of disparity and cues for accommodation). Interestingly, proximal vergence can be observed when an observer intends to fixate an object in the dark (Howard, 1995) or an object that is not seen. Moreover, vergence adjustments occur also when viewing twodimensional pictures that represent three-dimensional objects, as established by Enright (1987a,b) with participants viewing linear perspective drawings with one eye while vergence was measured from the other (non-stimulated eve).

In sum, we reasoned that if imagery emulates the embodied aspects of perception, pupils' size should consistently adjust when imagining familiar different-sized objects. In addition, larger objects (e.g., car) should dilate the pupil to a greater extent than smaller objects (e.g., dart), as occurs when viewing relatively smaller or larger patterns at the same distance (e.g., Daniels, Nichols, Seifert, & Hock, 2012). Moreover, the pupils' size should adjust when imagining these objects at relatively short distances than relatively far distances, in essence, emulating the pupillary near response (PNR). Moreover, as vergence is measurable concurrently with pupillometry by use of modern eye-tracking equipment, we expected to be able to register such an oculomotor response to accompanying

pupillary changes during imagery. Thus, we expected that the eyes would diverge more when imagining large and/or distant objects than when visualizing small and/or near objects. Based on previous studies showing that the effects of imagery are weaker than in perception (e.g. Laeng & Sulutvedt, 2014; Pearson et al., 2015), we expected to find effects in a similar direction as seen in perception, as a form of emulation, but not necessarily effects equal to what is seen in perception, as imagery and perception share similar neural substrates, while different network dynamics are involved (Lee, Kravitz, & Baker, 2011). Thus, we would expect small vergence changes for an imagined scene given that imagining an object while binocularly looking at a blank screen (of an eye-tracker) should partially suppress the vergence adjustments. Indeed, Enright (1987a,b) reported a tendency toward "vergence shortfall" when observers viewed depth cues in twodimensional drawing, although they were consistent with the direction in depth implied by the monocular depth cues. Pupil adjustments to illusory brightness or mental scenarios (e.g., Laeng & Endestad, 2012; Laeng & Sulutvedt, 2014) may be "anticipatory" or "preparatory" to a probable perceptual scenario (Zavagno, Tommasi, & Laeng, 2017) and typically represent a fragment of the appropriate adjustments of the pupil diameter to actual, physical brightness or illumination. In addition, as Pearson et al. (2015) proposed, visual mental imagery can be characterized as a weak or noisy form of top-down perception that can in some cases take the place of bottom-up perception; indeed, the MR signals during imagery of an object are typically weaker, though impressively similar, to those during perceiving the same object (Naselaris, Olman, Stansbury, Ugurbil, & Gallant, 2015).

Specifically, given that objects of different size would occupy very different portions of the visual field when seen at same distances, we considered that a small object (e.g., a clothespin) seen (or imagined) at a distance of 30 cm to be "near," whereas the same object seen (or imagined) at 4 m to be "far" away; in contrast, we considered a large object (e.g., an SUV) that is seen (or imagined) at 4 m to be "near," whereas the same object seen (or imagined) at 20 m to be "far" away (as illustrated below in Fig. 1).

2. Methods and materials

2.1. Participants

Forty-five participants (23 females, $mean\ age = 26.8\ years;\ SD = 8.82$) with normal to corrected-to-normal vision were recruited at the University of Oslo and from the local community. One participant was excluded from the analyses due to poor calibration and missing data entries. All participants signed a written consent form and were treated according to the Declaration of Helsinki.

2.2. Stimuli

The stimulus set included 24 color digital images: half for the "large" objects condition (i.e., armchair, billiard table, bunkbed, bus, car, cow, helicopter, hot air balloon, jukebox,

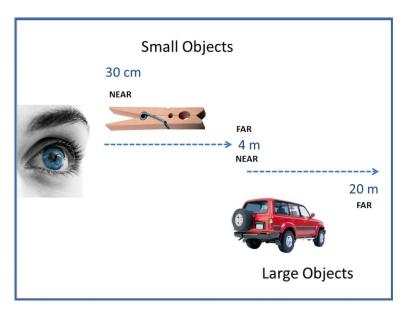


Fig. 1. Illustration of small and large objects imagined at relatively near and far distances. An object to be imagined (e.g., a clothespin or a SUV) was first shown at an approximately constant size on screen and, in different trials, the object was visually imagined at either 30 cm (relatively "near") versus 4 m (relatively "far") if a "small" object, whereas a "large" object was imagined at either 4 cm (relatively "near") versus 20 m (relatively "far").

soda machine, tractor, triumphal arch) and half for "small" objects (i.e., clothes' peg, cup, dart, hotdog, ipod, keys, nectarine, pepper shaker, ring, safety pin, teabag, watch). All the images were taken from the OBJECT 100 Database (http://konklab.fas.harvard.ed u/#). The object images were divided into "large" and "small" sets. Each image was fitted within white frames of similar sizes (i.e., Large $M = 10.91^{\circ}$, $SD = 1.93^{\circ}$) and (Small $M = 9.80^{\circ}$, $SD = 2.18^{\circ}$). Both conditions were blocked in counterbalanced order across participants and started with a practice image (e.g., a horse in the large condition and a mobile telephone in the small condition). The practice images contained more detailed instructions ("press the space bar when you have the image in mind"), which were not present through the rest of the experiment. In addition, basic imagery tasks ("imagine the object") with no instruction of distance were used to facilitate the later imagery of the objects and were thus not used in the analysis.

2.3. Procedure

A 2 (small/large objects) \times 2 (near/far) mixed design was used for the study. Prior to the experiment, each distance that was later to be visualized was demonstrated by the experimenter standing at 4 m and 20 m, for 15 s at each distance, using previously marked positions. The 30 cm distance was demonstrated through a standard tape measure. Participants were then seated 60 cm from a SMI RED 500 infrared eye-tracking device

(SensoMotoric Instruments[®], Germany), with a display resolution of $1,680 \times 1,050$ pixels. Data were recorded at a rate of 120 Hz, with a resolution >0.1°, and minimum gaze point accuracy of 0.5°. The head was stabilized to avoid movements, and distance to the screen was secured, through the use of a chinrest.

After a standard 4-point calibration procedure, an image was shown at the center of the screen for 5,000 ms as a "cue" for imagery in each trial, after which the participants were instructed to simply imagine the objects with no instructions of distance (5,000 ms). An epoch of 5 s was deemed sufficient to yield not only reliable pupillary diameters, as shown in previous studies (e.g., Laeng & Sulutvedt, 2014), but also reliable vergence changes considering that these movements are rather slow (about 25°/s) compared to the 500°/s velocity of saccade movements (Abrams, Meyer, & Kornblum, 1989). The basic imagery task was then followed by an empty gray baseline-screen (1,000 ms) and then written instructions succeeded over the same gray background telling the participants to imagine the previously seen object at a specific distance: either a "near" distance of 30 cm and 4 m for small and large object, respectively, or at a "far" distance of 4 m and 20 m for small and large objects, respectively. Participants pressed the spacebar when the mental image was clear in mind, which caused the same gray screen to reappear. Pupils were then registered for 5,000 ms during the imagery task, followed by a "stop" slide. The experiment lasted about 15 min, and the participants were compensated for their time (100 NOK).

All pupil data were baseline-corrected by subtracting the mean pupil size at "baseline" from the corresponding "imagery," thus obtaining a variable called "pupillary change." Vergence were calculated from the vectors' data which are provided as output by the SMI eye-tracking system (see http://www.euclideanspace.com/maths/algebra/vectors/angle Between/). The vectors provide the locations of the right and left eye independently, also in depth. Statistical analysis were performed with SPSS Statistics 24.

3. Results

3.1 Pupils

A repeated measures anova showed significant effects of Distance (near/far) on mean pupillary change during imagery, F(1, 43) = 4.45, p = .037, $\eta_p^2 = 0.10$, and Size (small/large), F(1, 43) = 4.04, p = .051, $\eta_p^2 = 0.09$. Similar results was found by item: Distance F(1, 23) = 8.54, p = .008, $\eta_p^2 = 0.27$ and Size F(1, 22) = 5.95, p = .023, $\eta_p^2 = 0.21$. As expected, pupils were on average larger when imagining distant objects (M = 0.22, SD = 0.21) than near objects (M = 0.17, SD = 0.18). Also as expected, pupils were on average smaller when imagining small objects (M = 0.18, SD = 0.17) than large objects (M = 0.22, SD = 0.21).

An interactive effect of Distance and Size was also found, F(1, 43) = 6.96, p = .012, $\eta_p^2 = 0.14$. A repeated-measures anova by item on distance with size as between-item factor showed a similar result F(1, 22) = 25.94, p = .000, $\eta_p^2 = 0.54$. The small objects

imagined at a "near" distance resulted in relatively smaller pupils compared to all other conditions (see Fig. 2A). Paired t-tests showed a significant difference between imagining small objects at a near versus far distance: M change = -0.10, SD = 0.25, t(43) = -2.71, p = .010, d = 0.58. However, pupils did not differ when imagining large objects at a near versus far distance: M change = 0.01, SD = 0.15, t(43) = 0.42, p > .250 (see Fig. 3B). The pairwise comparisons showed a significant difference between large and small objects imagined at a near distance: M change = 0.09, SD = 0.22, t (43) = 0.08, p = .008, d = 0.60, which as expected consisted in larger pupils when imagining the large objects. However, pupils when imagining large and small objects at a far distance did not differ significantly, M change = -0.02, SD = 0.13, t(43) = -0.87, t = 0.250 (see also Fig. 4). There was also no difference between small objects at a far distance and large objects at a near distance, t = 0.008, t = 0.16, t = 0.31, t = 0.76, that is, when imagining these objects at a same distance of 4 m.

3.2 Vergence

We first obtained from the vectors' data the mean radians values and then the visual angles for each participant in each condition. A repeated-measures ANOVA of ocular vergence during imagery revealed significant effects of Distance, F(1, 43) = 18.46, p < .001, $\eta_p^2 = 0.30$, and Size F(1, 43) = 18.71, p < .001, $\eta_p^2 = 0.30$. As expected, the angles were smaller when imagining distant objects (M = 5.50, SD = 2.02) than near objects (M = 6.23, SD = 1.78). Also as expected, the angles were larger when imagining small objects (M = 6.47, SD = 2.0) than when imagining large objects (M = 5.26, SD = 2.09).

There was also an interactive effect between Distance and Size, F(1, 43) = 12.57, p = .001, $\eta_p^2 = 0.23$ (see Fig. 2B). Paired *t*-tests revealed a significant difference between small (M = 5.87, SD = 2.12) and large (M = 5.14, SD = 2.32) objects imagined at a far distance: M change = 0.73, SD = 1.9, t(43) = 2.6, p = .013, d = 0.56, as well as a significant difference between small (M = 7.1, SD = 2.25) and large objects (M = 5.3, SD = 1.95) imagined at a near distance: M change = 1.7, SD = 2.25, t(43) = 4.99, p < .001, d = 1.08. The difference in vergence between small objects imagined at a near and far distance was significant: M change = 1.21, SD = 1.8, t(43) = 4.51, p < .001, d = 0.97. The was no significant difference between large objects imagined at a near and far distance: M change = 0.24, SD = 0.99, t(43) = 1.61, p = .116.

4. Discussion

Several aspects of the results were consistent with the hypotheses, since we found that (a) pupils were smaller during imagery of small objects than large objects, while (b) objects imagined at a far distance evoked greater pupillary dilations than when imagined at a near distance. Also, (c) the pupils dilated relatively more during imagery of small objects visualized at a relatively far distance than at a "near" distance. No evidence was found for effects of distance on pupillary changes in response to images of large objects.

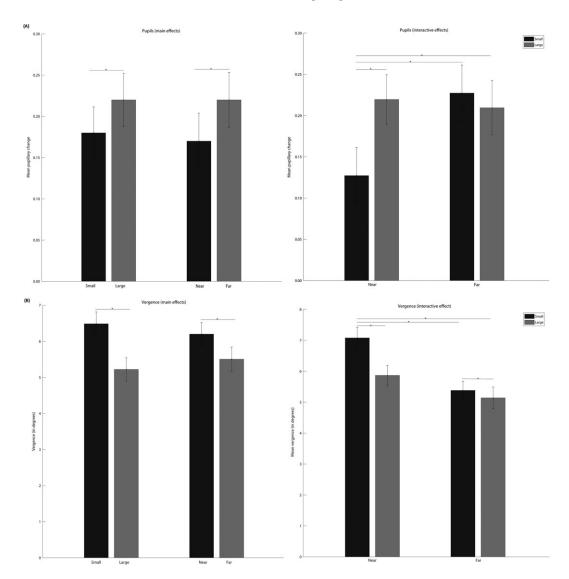


Fig. 2. (A) Mean pupillary change as a function of imagined small, large, near and far objects (main effects), and small and large objects at relatively near and far distance (interactive effect). (B) Mean vergence in degrees (the angle subtended by the eyes' direction of gaze) while imagining small, large, near, and far objects (main effect), and small and large objects at a near and far distance (interactive effect). *Indicate significance. Error bars indicate SE.

In addition, (d) the visual angle was larger when imagined at a near distance and smaller at a far distance. Consistently, (e) we registered systematic changes in the eyes' "vergence" in small objects imagined near and far, despite the requirement that participants had to focus on a blank screen positioned at a 60 cm distance that did not correspond to

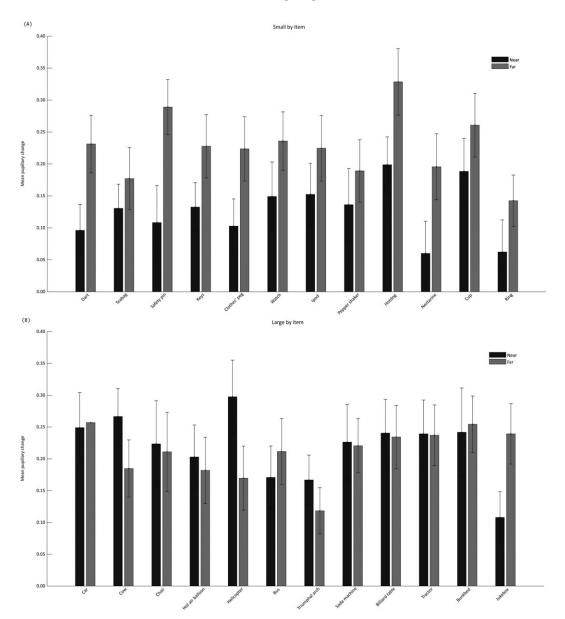


Fig. 3. Mean pupillary change as a function of (A) imagined small items near and far and (B) imagined large items near and far. Error bars indicate SE.

any of the imagined distances. Again, there was no significant difference in pupil diameter between large objects imagined relatively near or far.

A previous study by Daniels et al. (2012) measured pupillary changes while participants either controlled the scope of attention over a narrow pattern of dots (having a distance of 2.6° from one another) or the same dots at larger distance (26° from one another) and

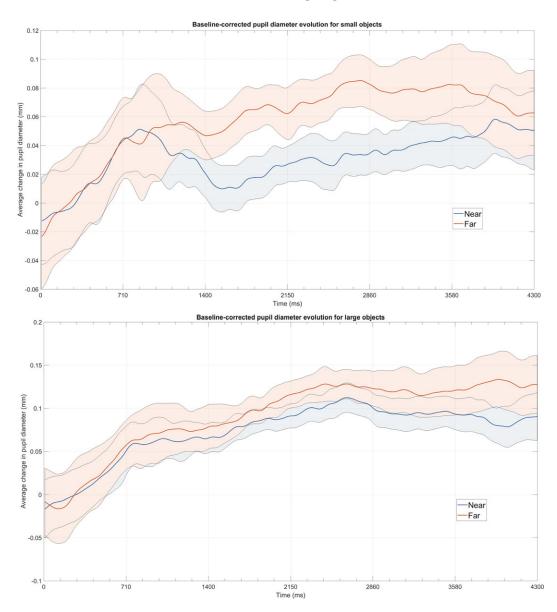


Fig. 4. Average pupil diameter change over time for "small" objects (top panel) and "large" objects (bottom panel) imagined near (blue line) and far (orange line). The colored patches show within-subject confidence intervals.

therefore over a larger region of space. In another experiment, the patterns either dynamically increased or decreased in size over a period of 2.5 seconds on screen (therefore, without change in distance). In both experiments Fourier analysis of the fluctuating pupil diameter indicated that the pupil diameter changed with the scope of attention, dilating with

broadly spread attention and contracting with narrowly focused attention. Interestingly, as shown in figure six in Daniels et al.'s (2012, p. 10), when observers saw the pattern enlarging on screen, the pupil diameter increased over time — pupil diameter was larger than the baseline after a period of 1.5 seconds. Conversely, when observing the pattern becoming smaller on screen, the pupil diameter decreased over time and after approximately 1 second was below baseline. Moreover, the average pupillary change from baseline reached a maximal value of about 0.5 mm (based on the graph in figure six in Daniels et al., 2012) in the large pattern condition and a minimum of about -0.4 mm in the small pattern condition.

In the present experiment with only imagined objects, the changes in pupil diameter observed during imagery of small versus large object were of about 1.0 mm on average in the near condition, which likely corresponded to larger changes in visual angle between small and large stimuli than those in Daniels et al.'s study with visible displays. Moreover, pupil changes (as illustrated in the curves of Fig. 4) clearly separated when imagining far and near objects at about 1.5 seconds from after receiving the instruction to generate a mental image. It is likely that on average 1.5 seconds is required to generate the mental image, and pupil adjustments follow once the mental image is fully represented.

Another recent study by Feil, Moser, and Abegg (2017) also recorded pupil size and vergence eye movements with the use of an infrared eye tracker after gaze shifts from far to near and compared the simultaneous pupil response to the response to a gaze shift from one far target to another. Feil and colleagues concluded that the main trigger for the pupillary response seemed to be convergence, since proximity alone did not induce a significant pupillary constriction and therefore miosis may be closely coupled to the vergence system rather than being independently regulated. On this account, one could surmise that the pupillary changes measured in the present experiment during imagery were also mainly triggered by the presence of consistent vergence responses. However, albeit vergence and pupillary changes were greatly concordant in the present findings, we did observe dissociations between pupil size and vergence during imagery. In particular, we found significant vergence differences between small and large objects (Fig. 2B, right panel), so that the eyes diverged more to large objects than small ones when these were imagined relatively far; yet there was no significant change in pupil size in the same condition (Fig. 2A, right panel).

Interestingly, Enright (1987a,b) had reported investigations of vergence as well as pupil responses while participants viewed line drawings and artwork that contained monocular cues to depth (e.g., linear perspective). An interesting aspect of Enright's experiments is that the participants viewed the stimuli with one eye while vergence was measured from the other (non-stimulated eye). There were clear but small converging – divergence changes consistent with viewing "closer" or "further away" parts of the represented objects or scenes, despite these properties were only implied by two-dimensional features on a same depth plane. Interestingly, Enright reported a tendency toward "vergence shortfall," in that the vergence changed consistently with the depth cues, but it did not incorporate a perfect readjustment. Surprisingly, the other component of the "near reflex" (Semmlow & Hung, 1983), a pupillary miosis to "close objects" was absent in this

study (Enright, 1987a), which may, however, reflect the small number of participants in these studies. Enright also suggests that adjustments of the oculomotor system triggered by depth cues may occur during ordinary, day-to-day perception. When interpreting a two-dimensional representations of three-dimensional objects and scene, these small converging-divergence changes may explain the subjective impression of depth while assisting "simulating" the spatial structure of the scene. Although the tendency to adjust vergence would be overridden by binocular fusion, Enright (1987a, p. 745) suggests that (a) even small changes in the appropriate directions would be associated with subjective appreciation of the implied depth and (b) that Claparède (1904) might have been right in suggesting that the "paradoxical monocular stereopsis" (e.g., when viewing a linear perspective representation with one eye only) might result from these "reflexive" oculomotor adjustments that are in part suppressed when viewing with both eyes. Although Enright's studies did not investigate imagery, we cannot exclude that also in his paradigm imagery might have interacted and augmented the perception (cf. Karimpur & Hamburger, 2018; Neisser, 1976). Indeed, we speculate that both when viewing drawings and paintings (with only monocular cues to depth) and in mental imagery (with no cues at all), the embodied oculomotor "near reflex" will assist generating the appropriate perceptual simulation in three-dimensional mental space.

Another hint that vergence responses during imagery may not be the main trigger for the pupillary response to imagined size is that, in the present experiment, the observed changes in vergence appear to be narrower in magnitude and variance than those one would expect to occur during perception. Specifically, focusing the eyes on a point at 30 cm of distance and assuming an average interpupillary distance of about 6.5 mm (Chelnokova & Laeng, 2011; Dodgson, 2004), one would expect that the angle of vergence of the eyes would correspond to about 14°; in contrast, when focusing the eyes on a point at 4 m of distance, one would expect a vergence of about 1.5°. Instead in this study, vergence never surpassed angles of 7° and varied across condition by about 1°. Nevertheless, the observed vergence changes were rather consistent with the expected direction of change and this aspect may be the most relevant when considering the present vergence findings in imagery. Indeed, illusory or imaginary stimuli generally tend to produce weaker effects than the actual stimuli, probably because these effects reflect preparatory mechanisms to predicted stimuli and the concurrent sensory input acts to suppress part of the response. In the present case, we need to stress that the pupils were stimulated by constant light levels, but the vergence movements were constrained by the presence of a physical occluder (the computer screen) at a constant distance, especially when imagining objects beyond the occluder. Remarkably, the screen was positioned at 60 cm so that the angle of vergence when looking on a point on screen, assuming an interpupillary distance of about 6.5 mm, would correspond to about 7°; that is, very close to our measured vergence which varied between 5° for far and large objects and 7° for near and small objects (see Fig. 2B). This reinforces the idea that the plane of the screen was an attractor for gaze and it constrained variation in vergence only toward empty, unoccluded positions in front of the screen.

Surprisingly, both small and large objects resulted in similar, relatively large dilations when imagined from a far distance, and these did not differ from pupillary changes in response to small objects imagined at a far distance. One possibility is that, in the present experiment, participants first viewed on-screen actual images of the objects they were to imagine, which may have influenced the participants to imagine the large objects as smaller than they normally are. Research has shown that previous knowledge of an objects size leads to differences between imagery of those objects from memory and imagery of objects from just-seen pictures. Objects from just-seen pictures are imagined as smaller than in comparable imagery from memory (Kosslyn, Ball, & Reiser, 1978; Mitchell & Cusack, 2016). It is also possible that some of the large objects may have overflowed the visual angle of the mind's eye (i.e. Kosslyn, 1978) at both 4 m and 20 m distance (e.g., the Paris triumphal arch's real size is 50 m high and 45 m wide), and the inability to represent the whole image might have constrained the adjustments of the pupil. However, removing from analyses the three items that would most likely overflow at a 4 m distance (i.e., the bus, air balloon and triumphal arch) did not change the direction and significance of the present effects. As visualized in Fig. 3, most large objects elicited similar pupil response whether imagined from near or far (only bus and jukebox were in the expected direction), except cow, helicopter, and triumphal arch, which elicited a clear opposite effect; that is, the pupils dilated more to these large objects imagined near and less when imagined far away. An explanation may be that the participants imagined the large objects in a more variable manner than the small object. Six of the large objects, unlike the small objects, are often seen in motion (bus, car, cow, helicopter, hot air balloon and tractor), which may be a contributing factor. Hence, seeing for instance a helicopter or cow in motion at a 4 meter distance (especially if coming toward you) may be scary, and we did not specify to imagine that the objects were standing still. Moreover, a helicopter and hot air balloon are usually seen at a very far distance (further away than 20 m), and this may also apply to cows if you have only seen cows on the field from for instance a car in motion. Also well-known objects, like an armchair, may vary considerably in size, and combined with the notion that "objects you have at home" may be easier to imagine, this may cause substantial variations in imagery. These differences may have resulted in greater variability in how objects in the large condition were imagined, influencing in turn both pupil dilations and vergent eye movements. Interestingly, Mitchell and Cusack (2016) found that the occipital cortex can clearly represent properties of formally encoded images during imagery, but these representations and their content depend on individual diversities in imagery style, the object that was to be imagined, and subjectively reported vividness of imagery. In fact, they found no consistent representation of imagery when the participants imagined a dolphin, which can be imagined up close, from a far distance, in a still picture, or in motion. Also, how well acquainted people are with the specific objects they are asked to imagine may influence the vividness of imagery (e.g. Kousta, Vigliocco, Vinson, Andrews, & Del Campo, 2011). As we mostly tested young students at the university, they may have been more familiar with the small items, like cups, darts, keys, and hot dogs, than they were with, for instance, cows, helicopters, and tractors, and some of them might have never seen a hot air balloon or a triumphal arch.

Another possibility is that the present pupillary changes reflect the ongoing effort in generating the image more than the spatial properties of the objects involved. Pupillary changes have been shown to provide a reliable measure of mental effort (e.g., Alnæs et al., 2014), as originally proposed by Kahneman (1973). In light of this idea, then it would seem that imagining the small objects at 30 cm may be less effortful in general than imagining large objects at 4 m and 20 m. The participants in the current experiment were seated at a table inside a small room, and small objects used in this experiment are usually seen inside a small room (e.g., a cup is typically on top of a table). In this case, imagining large objects usually seen outside and at further distances may have been more challenging than imagining the small objects. In fact, Peavler (1974) has shown that when a task becomes increasingly effortful at the point of overload, not only does performance drop but the pupil decreases in size relative to the pupil response during effortful conditions with high performance.

There were nevertheless several limitations in this study. First of all, the relative sizes within the large condition were not consistent, containing objects ranging from the size of a cow (approximately 1.5 to 1.8 meters high and 1.5 meters long), to the arc de triumph. While this should not make a difference in terms of vergence or pupillary activity, it would seem appropriate in later studies to ensure all objects to be within a specific predetermined size range. In order to avoid the potential constrictions of imagery of large objects at a distance while fixating on a screen, while seated in a small room, future studies could make use of mobile eye-tracking equipment as this would allow for conducting the experiment without occluders and possibly in full darkness (for better controlled pupillometry measurements, since gradients of illumination dependent on distance are unavoidable within a large room). Moreover, future studies would benefit from including a questionnaire of how much effort it took to imagine the different objects from the various distances, and how vivid the image was in mind. In this study, if bodily responses during imagery improve the function of imagery, the imagery of the large objects may have been less vivid than the imagery of the small objects.

Finally, we note that several studies suggest that a (real-world) canonical size is associated to both imagined and viewed visual objects (Konkle & Caramazza, 2013; Konkle & Oliva, 2011, 2012). However, other studies (e.g. Mitchell & Cusack, 2016) observed a reduction in object size in imagery from former encoded images and suggest that this phenomenon reflects the lack of impending physical interaction with the imagined object. In addition, object's size, which is crucial to estimate distance during perception, may not be necessary during imagery. However, the present experiment shows an effect of size, distance and an interaction effect between size and distance during imagery as reflected in both pupil size and vergence eye movements, implying that both size and distance are relevant to imagery, as formerly suggested by Kosslyn (1978). Moreover, the present evidence supports the idea that the nature of imagined mental space is three–dimensional, as it had already been implied by previous mental rotation studies of shapes in different planes (e.g., Peters et al., 1995; Shepard & Metzler, 1971; Vandenberg & Kuse, 1978).

In conclusion, the present findings are consistent with the idea that imagery emulates perception by affecting activity in the eye itself. In turn, they suggest that the process of imagery may depend upon bodily responses or that these improve its function, as predicted by the theory of embodied cognition. Indeed, oculomotor adjustments like the ones described here and elsewhere (e.g., eye fixations and scanpaths; e.g., Laeng et al., 2014) have provided evidence for the idea that mental imagery re-represent perception and recruits the same sensory-motor processes automatically whenever mental images are conjured up. In the present investigation, we found that both the pupil diameter and eyes' vergence adjusted to what participants imagined seeing instead of the actual input sensed by the eye (i.e., an occluding screen at a fixed distance and no visible object), especially during imagery of the small objects. Within current theories in cognitive science (neuroscience), such physiological adjustments during visual imagery can be accounted for by a view that assumes our brain functions as a (Bayesian) statistical machine that predicts visual content over and above the information provided by the visual input. That is, biology may have equipped our neural networks with strategies that optimize visibility of impending events — even when these are imagined or illusory — so that an individual can react efficiently (e.g., glare and dazzle; Laeng & Endestad, 2012; Laeng et al., 2018; Zavagno et al., 2017). Indeed, we seem to be ready to counteract such predicted states of the world by preparing our optical sensors by adjusting the size of the pupils in time.

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Conflict of interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

References

- Abrams, R. A., Meyer, D. E., & Kornblum, S. (1989). Speed and accuracy of saccadic eye movements: Characteristics of impulse variability in the oculomotor system. *Journal of Experimental Psychology: Human Perception and Performance*, 15(3), 529–543. https://doi.org/org/10.1037/0096-1523.15.3.529.
- Alnæs, D., Sneve, M. H., Espeseth, T., Endestad, T., van de Pavert, S. H., & Laeng, B. (2014). Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *Journal of Vision*, *14*(4), 1–20. https://doi.org/10.1167/14.4.1.
- Brandt, S. A., & Stark, L. V. (1997). Spontaneous eye movements during visual imagery reflect the content of the visual scene. *Journal of Cognitive Neuroscience*, 9(1), 27–38. https://doi.org/10.1162/jocn.1997.9.1. 27.

- Chelnokova, O., & Laeng, B. (2011). Three-dimensional information in face recognition: An eye-tracking study. *Journal of Vision*, 11(13), 27.
- Claparède, E. (1904). Stéréoscopie monoculaire paradoxale [Paradoxical monocular stereopsis]. *Annales d'Oculistique*, 132, 465–466.
- Daniels, L. B., Nichols, D. F., Seifert, M. S., & Hock, H. S. (2012). Changes in pupil diameter entrained by cortically initiated changes in attention. *Visual Neuroscience*, 89(2), 197–202. https://doi.org/10.1017/ S0952523812000077.
- Dodgson, N. A. (2004). Variation and extrema of human inter-pupillary distance. In A. J. Woods, J. O. Merritt, S. A. Benton & M. T. Bolas (Eds.), *Proceedings of SPIE: Stereoscopic displays and virtual reality systems XI* (vol. 5291, pp. 36–46). San Jose, CA: Society of Photo-Optical Instrumentation Engineers (SPIE).
- Enright, J. T. (1987a). Perspective vergence: Oculomotor responses to line drawings. *Vision Research*, 27(9), 1513–1526. https://doi.org/10.1016/0042-6989(87)90160-X.
- Enright, J. T. (1987b). Art and the oculomotor system: Perspective illustrations evoke vergence changes. *Perception*, 16(6), 731–746. https://doi.org/10.1068/p160731.
- Feil, M., Moser, B., & Abegg, M. (2017). The interaction of pupil response with the vergence system. *Graefes Arch Clin Exp Ophthalmology*, 255(11), 2247–2253. https://doi.org/10.1007/s004117-017-3770-2.
- Fincham, E. F., & Walton, J. (1957). The reciprocal actions of accommodation and convergence. *The Journal of Physiology*, 137(3), 488–508. https://doi.org/10.1113/jphysiol.1957.sp005829.
- Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic simulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, 10(2), 175–180. https://doi.org/org/10. 1093/cercor/10.2.175.
- Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research*, 20(2), 226–241. https://doi.org/10.1016/j.cogbrainres.2004.02.012.
- Hebb, D. O. (1968). Concerning imagery. *Psychological Review*, 75(6), 466–477. https://doi.org/org/10.1037/h0026771.
- Higashiyama, A., & Adachi, K. (2006). Perceived size and perceived distance of targets viewed from between the legs: Evidence for proprioceptive theory. *Vision Research*, 26(23), 3961–3976. https://doi.org/org/10.1016/j.visres.2006.04.002.
- Howard, I. P. (1995). Binocular vision and stereopsis. Oxford, UK: Oxford University Press.
- Jampel, R. S. (1972). The control of eye movements. *Neurology*, 22(7), 770. https://doi.org/10.1212/WNL.22. 7.770.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17(2), 187. https://doi.org/10.1017/S0140525X00034026.
- Kahneman, D. (1973). Attention and effort. Englewood Cliffs, NJ: Prentice-Hall.
- Karimpur, H., & Hamburger, K. (2018). A rat in the sewer: How mental imagery interacts with object recognition. *PLoS ONE*, *13*(3), e0194227. https://doi.org/10.1371/journal.pone.0194227.
- Konkle, T., & Caramazza, A. (2013). Tripartite organization of the ventral stream by animacy and object size. *Journal of Neuroscience*, 33(25), 10235–10242. https://doi.org/10.1523/JNEUROSCI.0983-13.2013.
- Konkle, T., & Oliva, A. (2011). Canonical visual size for real-world objects. *Journal of Experimental Psychology: Human Perception and Performance*, 37(1), 23–37. https://doi.org/10.1037/a0020413.
- Konkle, T., & Oliva, A. (2012). A real-world size organization of object responses in occipitotemporal cortex. *Neuron*, 74(6), 1114–1124. https://doi.org/10.1016/j.neuron.2012.04.036.
- Kosslyn, S. M. (1978). Measuring the visual angle of the mind's eye. *Cognitive Psychology*, 10(3), 356–389. https://doi.org/10.1016/0010-0285(78)90004-X.
- Kosslyn, S. M. (1994). Image and brain. Cambridge, MA: The MIT Press.
- Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance*, 4(1), 47–60. https://doi.org/10.1037/0096-1523.4.1.47.

- Kousta, S. T., Vigliocco, G., Vinson, D. P., Andrews, M., & Del Campo, E. (2011). The representation of abstract words: Why emotion matters. *Journal of Experimental Psychology: General*, 140(1), 14–34. https://doi.org/10.1037/a0021446.
- Laeng, B., Bloem, I. M., D'Ascenzo, S., & Tommasi, L. (2014). Scrutinizing visual images: The role of gaze in mental imagery and memory. *Cognition*, 131(2), 263–283. https://doi.org/10.1016/j.cognition.2014.01. 003.
- Laeng, B., & Endestad, T. (2012). Bright illusions reduce the eye's pupil. *Proceedings of the National Academy of Sciences*, 109(6), 2162–2167. https://doi.org/10.1073/pnas.1118298109.
- Laeng, B., Kyambarua, K., Hagen, T., Bochynska, A., Lubell, J., Suzuki, H., & Okubo, M. (2018). The "face race lightness illusion": An effect of the eyes and pupils? *PLoS ONE*, 13(8), e0201603. https://doi.org/10.1371/journal.pone.0201603
- Laeng, B., & Sulutvedt, U. (2014). The eye pupil adjusts to imaginary light. *Psychological Science*, 25(1), 188–197. https://doi.org/10.1177/0956797613503556.
- Laeng, B., & Teodorescu, D. S. (2002). Eye scanpaths during visual imagery re-enact those of perception of the same visual scene. *Cognitive Science*, 26(2), 207–231. https://doi.org/org/10.1016/S0364-0213(01) 00065-9.
- Lee, S. H., Kravitz, D. J., & Baker, C. I. (2011). Disentangling visual imagery and perception of real-world objects. *NeuroImage*, 59(4), 4064–4073. https://doi.org/10.1016/j.neuroimage.2011.10.055.
- Martarelli, C. S., Chiquet, S., Laeng, B., & Mast, F. W. (2016). Using space to represent categories Insights from gaze position. *Psychological Research*, 81(4), 721–729. https://doi.org/10.1007/s00426-016-0781-2.
- Mast, F. W., Ganis, G., Christie, S., & Kosslyn, S. M. (2003). Four types of visual mental imagery processing in upright and tilted observers. *Cognitive Brain Research*, 17(2), 238–247. https://doi.org/org/10.1016/S0926-6410(03)00111-3.
- Mathot, S., Grainger, J., & Strijkers, K. (2017). Pupillary responses to words that convey a sense of brightness or darkness. *Psychological Science*, 28(8), 1116–1124. https://doi.org/10.1177/09567976177 02699.
- Mitchell, D. J., & Cusack, R. (2016). Semantic and emotional content of imagined representations in human occipitotemporal cortex. *Scientific Reports*, 6, 20232. https://doi.org/10.1038/srep20232.
- Moulton, S. T., & Kosslyn, S. M. (2009). Imagining predictions: Mental imagery as mental emulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1273–1280. https://doi.org/10.1098/rstb.2008.0314.
- Naselaris, T., Olman, C. A., Stansbury, D. E., Ugurbil, K., & Gallant, J. L. (2015). A voxel wise encoding model for early visual areas decodes mental images of remembered scenes. *NeuroImage*, *105*, 215–228. https://doi.org/10.1016/j.neuroimage.2014.10.018.
- Neisser, U. (1976). Cognition and reality: Principles and implications of cognitive psychology. New York: W H Freeman.
- Nigmatullina, Y., Arshad, Q., Wu, K., Seemungal, B. M., Bronstein, A. M., & Soto, D. (2015). How imagery changes self-motion perception. *Neuroscience*, 291, 46–52. https://doi.org/10.1016/j.neuroscience.2015.01.021
- Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental imagery: Functional mechanisms and clinical applications. *Trends in Cognitive Science*, 19(10), 590–602. https://doi.org/10.1016/j.tics.2015. 08.003.
- Peavler, W. S. (1974). Pupil size, information overload, and performance differences. *Psychophysiology*, 11 (5), 559–566. https://doi.org/10.1111/j.1469-8986.1974.tb01114.x.
- Peters, M., Laeng, B., Latham, K., Jackson, M., Zaiyouna, R., & Richardson, C. (1995). A redrawn Vandenberg and Kuse mental rotations test: Different versions and factors that affect performance. *Brain and Cognition*, 28(1), 39–58. https://doi.org/10.1006/brcg.1995.1032.
- Rouw, R., Kosslyn, S. M., & Hamel, R. (1997). Detecting high-level and low-level properties in visual images and visual percepts. *Cognition*, 63(2), 209–226. https://doi.org/org/10.1016/S0010-0277(97)00006-1.

- Ruggieri, V., & Alfieri, G. (1992). The eyes in imagery and perceptual processes: First remarks. *Perceptual and Motor Skills*, 75(1), 287–290. https://doi.org/10.2466/pms.1992.75.1.287.
- Semmlow, J. L., & Hung, G. K. (1983). The near response: Theories of control. In C. M. Schor (Ed.), Vergence eye movements: Basic and clinical aspects. London: Butterworths.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703. https://doi.org/10.1126/science.171.3972.701.
- de'Sperati, C. (2003). Precise oculomotor correlates of visuospatial mental rotation and circular motion imagery. *Journal of Cognitive Neuroscience*, 15(8), 1244–1259. https://doi.org/10.1162/089892903322 598184.
- Vandenberg, S. V., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, 47(2), 599–604. https://doi.org/10.2466/pms.1978.47.2.599.
- Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, 68(1), 77–94. https://doi.org/org/10.1016/S0010-0277(98)00032-8.
- Winawer, J., Huk, A. C., & Boroditsky, L. (2010). A motion aftereffect from visual imagery of motion. *Cognition*, 114(2), 276–284. https://doi.org/10.1016/j.cognition.2009.09.010.
- Zavagno, D., Tommasi, L., & Laeng, B. (2017). The eye pupil's response to static and dynamic illusions of luminosity and darkness. *i-perception*, 8(4), 1–15. https://doi.org/10.1177/2041669517717754