Current Biology

Dynamic Re-calibration of Perceived Size in Fovea and Periphery through Predictable Size Changes

Highlights

- Exposure to trans-saccadic size changes re-calibrates perceived size

- The re-calibration of perceived size is established quickly and is long lasting

- Re-calibration established at one location transfers to the opposite hemifield

- Re-calibration can also be induced without saccades through object motion

Authors

Matteo Valsecchi, Karl R. Gegenfurtner

Correspondence

karl.r.gegenfurtner@psychol.
uni-giessen.de

In Brief

Valsecchi and Gegenfurtner show that appearance of size is constantly calibrated on the basis of trans-saccadic prediction error. This leads to a stable appearance of the world, although the cortical representation of visual input differs dramatically between fovea and periphery.

CrossMark

CellPress

Cell Press

Dynamic Re-calibration of Perceived Size in Fovea and Periphery through Predictable Size Changes

Matteo Valsecchi[1] and Karl R. Gegenfurtner[1,*]
[1]Department of Psychology, Justus Liebig University Giessen, Otto-Behaghel-Strasse 10F, 35394 Giessen, Germany
*Correspondence: karl.r.gegenfurtner@psychol.uni-giessen.de
http://dx.doi.org/10.1016/j.cub.2015.10.067

SUMMARY

The same object produces quite distinct images in the cortical representation, depending on whether it is looked at foveally or with the periphery, yet some form of size constancy prevents us from experiencing objects inflating or deflating as we move our eyes. According to the prominent sensorimotor account of vision by O'Regan and Noë [1], we constantly learn to discount the predictable sensory effects of motor actions, such as the projection of a stimulus on a larger cortical area as it gets foveated. Although previous studies have shown that foveal and parafoveal inputs can be associated in visual memory [2, 3], trans-saccadic prediction error could in principle re-calibrate even the appearance of peripheral and foveal stimuli. Here we introduce a new paradigm that induces such changes in the relative appearance of peripheral and foveal stimuli when directly compared. Repeated exposure to a trans-saccadic change in size, though unnoticed by most observers, induced a substantial modification of perceived size that lasted at least 1 day. Prediction is not limited to the motor system but can also occur for the sensory effects of external events, such as stimulus motion. We show that perceptual re-calibration can occur in the absence of eye movements if the change in size occurs predictably while objects move across the visual field. Perceptual uniformity emerges due to the continuously updated prediction of foveal appearance based on peripheral appearance.

RESULTS AND DISCUSSION

Main Experiment: Re-calibration of Appearance

In each trial, observers first compared the size of two approximately circular stimuli: one viewed centrally and one viewed peripherally (Figure 1A). After giving their judgment, they made a saccade to the peripheral stimulus. During the saccade, its size could be decreased or increased by 10%. Over the course of the first session of the experiment, the trans-saccadic manipulation induced a corresponding change in the perceived size of the peripheral stimulus compared to the foveal one, as indexed by the change in the point of subjective equality (PSE) during

the course of the experiment (see Figure S1 and Supplemental Experimental Procedures for details). For example, after being exposed to a 10% decremental trans-saccadic radius change for 300 trials, the perceived radius of the peripheral stimulus decreased by 7% relative to the foveal stimulus, nearly matching the physical size change (Figure 1C). The curve from the increase group does not show an overall change. However, a comparison between both curves and the curve of the control group, who was not exposed to any trans-saccadic change, suggests that re-calibration was induced both by size increases and decreases. The reasons for this generic trend toward a PSE decrease in the first 200 trials is most likely the well-known tendency to report peripheral stimuli as appearing slightly smaller (e.g., [4]), coupled with our adaptive-staircase procedure, which can take a few dozens of trials before accommodating the stimulus range to a biased PSE.

On the second day, we reversed the manipulation for each group of observers, and accordingly, appearance was re-adjusted (Figure 1D). The perceived size adjustment can be summarized as the rates of size change (Figure 1E), which differed significantly between the decrease and increase groups on both days (day 1: t(30) = 3.724, p < 0.0016; day 2: t(30) = 5.219, p < 0.001; both Bonferroni corrected). As expected, it reversed between day 1 and day 2 (F(1,30) = 42.12; p < 0.001). Importantly, the initial PSE value differed between the groups on day 2 (t(30) = 3.04; p < 0.005), indicating a long-lasting effect of the training on the previous day. This could suggest that the learning is limited to the specific context in which it took place, in particular because similar learning phenomena [3, 5, 6] have been shown to be object specific. Notice however that saccadic adaptation, for example, is both context-independent (e.g., [7]) and long-lasting (e.g., [8]).

Post-session: Re-calibration Spreads to the Opposite Hemifield

In the experiment above, testing was performed only at the location where the size change was introduced. Perceptual learning processes were often shown to be entirely local [9], but recently there has been some evidence that generalization is possible in some cases [10, 11]. In order to investigate the possible transfer of re-calibration to untrained locations, 16 of the observers also underwent post-sessions, in which apparent size was tested without any further saccades. The observers judged size both at the location of the saccadic target during training and in the opposite hemifield and did not direct their gaze at the peripheral stimulus afterward. The corresponding PSE values, taking into account each observer's initial baseline level, are presented in
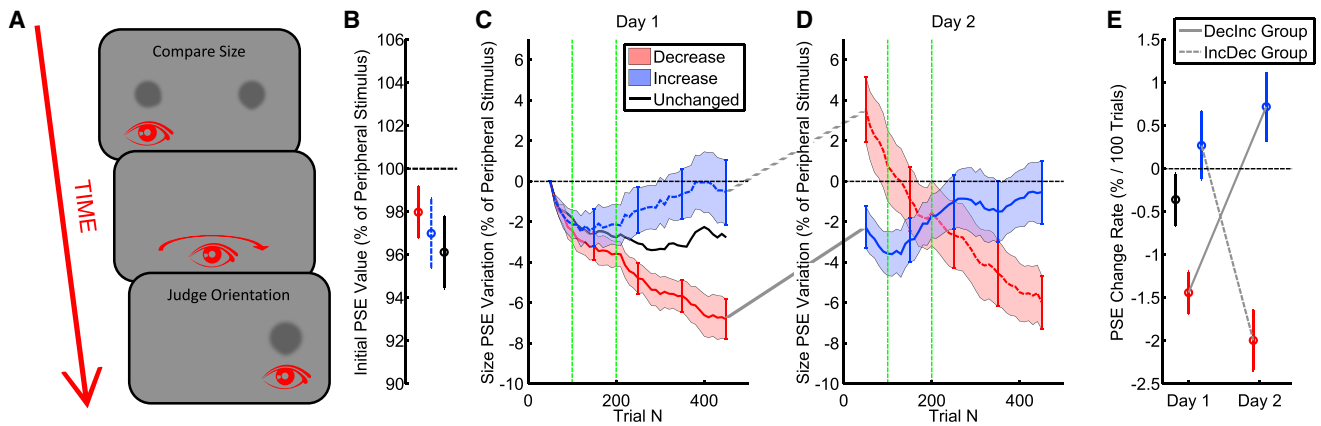
Figure 1. Experimental Task in the Main Experiment

(A) Experimental procedure. Observers first compared the size of the central and peripheral stimulus. Subsequently, they looked at the peripheral stimulus and judged its orientation. Both judgments and the eye movement were unspeeded. During the saccadic eye movement, the size of the stimulus could increase or decrease by up to 10%. See Supplemental Experimental Procedures for details.

(B–E) Time course of the change in perceived size (stimulus radius) throughout the main experiment.

(B) Initial value of the PSE computed in the first 100 trials where no trans-saccadic change took place is shown.

(C and D) Variation in the PSE relative to each observer's initial value is shown. The vertical green dashed lines denote the 100th trial, where the size change was introduced, and the 200th trial, where it reached its full extent of ±10%. Shaded areas and error bars are SEM. The colored error bars spaced by 100 trials denote size estimates computed on completely separate subsets of trials and thus independent, whereas intermediate estimates are computed on partially overlapping subsets of trials. After the 200th trial, the PSE values start diverging, indicating that the exposure to a manipulation of the post-saccadic size produces the predicted change in the pre-saccadic size appearance. Solid and dashed lines identify the decrease-increase and increase-decrease groups, respectively.

(E) Average rate of change in perceived size as a function of day is shown.

Figure 2. The results in the two post-sessions mirror quite closely the situation at the end of the preceding training sessions at both locations.

We submitted the PSE variation data to a three-way ANOVA (location: same versus different; group: DecInc versus IncDec; day: 1 versus 2). The group by day interaction was significant ($F(1,14) = 126.039$; $p < 0.001$), indicating that the effects of learning are still measurable when no saccades are performed. Crucially, the three-way interaction ($F(1,14) = 1.937$; $p = 0.186$), as well as all other main effects or interactions (all $p > 0.15$) were not significant. Overall, the results indicate that the learning is transferred equally to both sides of the visual field and is not local. Our size comparison method for testing appearance does not distinguish between changes in local size representation, whether foveal or peripheral, and changes to a more-general central-peripheral size-scaling mechanism. One possible reason for having a symmetrical size-scaling mechanism could be that cortical magnification predicts a relatively uniform geometrical distortion in cortical projection as a function of eccentricity [12–14]. This suggests that a relatively high-level perceptual mechanism is responsible for the trans-saccadic re-calibration. After all, whereas there is ample evidence associating perceived size to cortical projections starting from V1 [15–18], the trans-saccadic re-calibration process would be in place precisely to compensate for the geometrical distortions in early visual areas.

Reverse Change Experiment: No Re-calibration

The situation in our experiments closely mimics the dynamics of fovea-periphery associations in everyday life. First, we see an object in the periphery and then we make a saccade toward the object and see it foveally. In principle, we can also associate two objects in the reverse sequence. After the saccade, the object that was previously in the fovea is now in the periphery. A size change in this object during the saccade might lead to the same learning processes.

Another 16 observers were tested in a modified version of the paradigm. Like in the main experiment, the observers compared the size of a centrally viewed and a peripherally viewed stimulus, but after the saccade, the saccadic target disappeared and the previously fixated stimulus was still visible in the periphery where its size could be modified. Between 50 and 1,050 ms following the re-appearance of the now peripheral stimulus, its shape changed for one frame (16 ms) to an oriented shape similar to the ones used in the other experiments. Observers were informed that this change could only occur in this time frame, so that, if they had not perceived any change relatively soon after stimulus onset, they were supposed to guess its orientation. Given that preliminary data suggested that the oriented stimulus might be less visible if presented just after the saccade, four separate staircases determined the amplitude of the oriented protrusion based on the its onset delay (50–300, 300–550, 550–800, and 800–1,050 ms).

Unlike the exposure to a trans-saccadic change in the saccadic target size, the change in the formerly fixated stimulus failed to induce any systematic re-calibration of perceived size (see Figure 3). In order to perform an overall test for the presence of re-calibration, we submitted the rate of change values to a two-way ANOVA with group (IncDec versus DecInc) and day (1 versus 2) as factors. None of the main effects nor the two-way interaction turned out significant (all $p > 0.3$), suggesting that the exposure to modified peripheral feedback did not modulate the spontaneous tendency to PSE decrease. Notice that the non-significant numerical trend for an interaction observed in
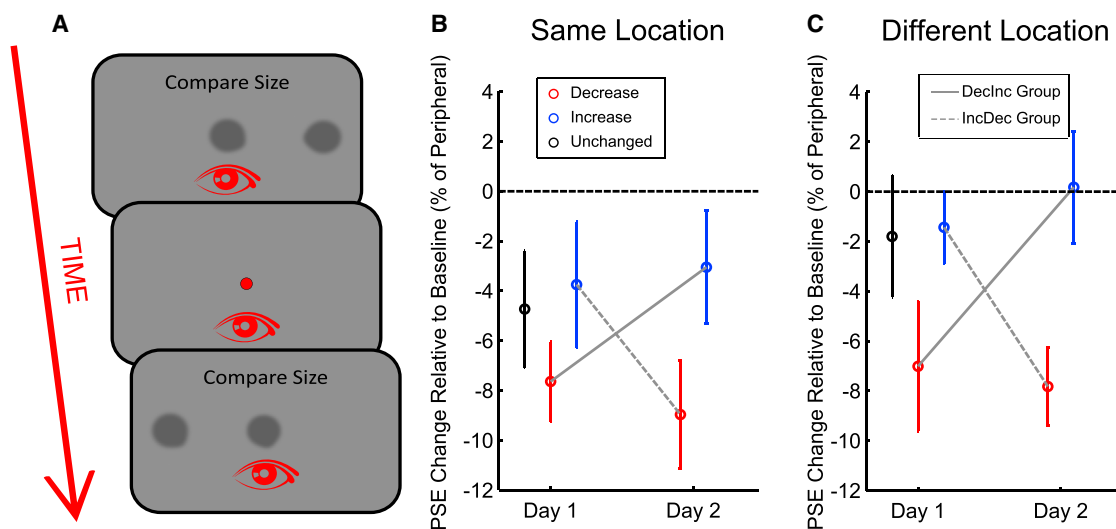
Figure 2. Procedure and Perceived Size Values in the Post-sessions

PSE values are expressed as change relative to baseline. In the post-session, the peripheral stimulus appeared alternatively on the same side where it had appeared during the training session (data in B) and on the opposite side (data in C) and the observers did not execute any saccades or orientation judgments. The effect of the training seems still evident in the post-tests; notice in particular how the relative magnitude of the PSEs is reversed between day 1 and day 2 across groups. Moreover, there is no evidence that the effect of learning is stronger when the trained hemifield was tested as opposed to the untrained one.

Figure 3 is the opposite of what would be expected had re-calibration taken place. An increase in the size of the stimulus between foveal and peripheral vision would have induced a relative reduction in the perceived size of the peripheral stimulus had re-calibration taken place. We further submitted the rate of change data from the main experiment and from the reverse change experiment to a combined three-way ANOVA with day (1 versus 2) as a within-observers factor and group (IncDec versus DecInc) and experiment (main versus reverse re-calibra-
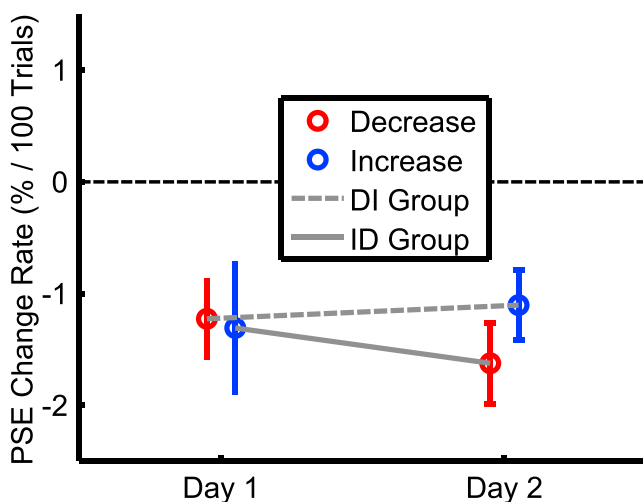

Figure 3. PSE Change Rates in the Reverse Re-calibration Experiment

No clear evidence of reverse re-calibration was observed. Notice that because the increase and decrease labels refer to a change between foveal and peripheral vision, the expected PSE change would have been the opposite of the one observed in the main experiment (Figure 1E).

tion) as between-observers factors. This yielded a significant three-way interaction ($F(1,44) = 22.88$; $p < 0.001$), confirming that there is less—if any—re-calibration in the reverse change experiment.

Objects that are viewed peripherally after the saccade do not influence size perception. One explanation of the discrepancy between this result and what we observed when we changed the size of the saccadic target might be in terms of attention. It is well known that visual attention is to a large degree bound to the saccadic target [19]. Therefore, fewer resources might have been allocated to the previously fixated stimulus, even though our observers were explicitly required to keep tracking its possible shape variations.

Stimulus Motion Experiment: Re-calibration without Saccades

We execute saccades several times per second, and therefore, saccades are presumably the main cause of association between peripheral and foveal targets. They are, however, not the only potential cause. Object motion can cause such associations whenever an object moves from the visual periphery into the fovea, or vice versa.

A further set of 16 observers was tested in a variation of the paradigm, in which, after the usual size judgment, the observers did not execute a saccade, but the peripheral stimulus moved to the fixated location (Figure 4A; Supplemental Experimental Procedures).

The results show that the stimulus size change occurring during its motion toward the fovea did also produce some re-calibration of perceived size. In particular, the relative value of the PSE rate of change between the groups reverses between day 1 and day 2, according to the reversal of the size manipulation. Notice the similar pattern in Figure 4 and in Figure 2. This was confirmed by a two-way ANOVA with day (1 versus 2) and
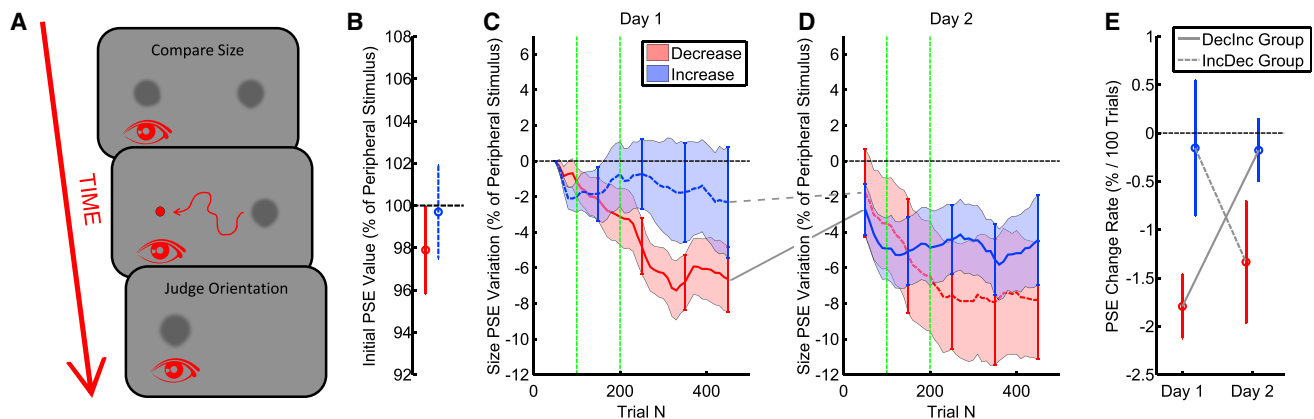
Figure 4. Procedure and Perceived Size Modulation in the Stimulus Motion Experiment

All conventions are as in Figure 1. The procedure is identical to the one of the main experiment, except that the observers do not shift gaze and the stimulus moves toward the fixation point instead. As evidenced by the interaction in (E), the PSE change rate is affected by the size change that took place during the movement; notice the similarity with the pattern in Figure 1E. The re-calibration taking place on day 1, however, does not seem to affect the initial value at the beginning of the testing on day 2 (D).

group (IncDec versus DecInc) as factors, in which the two-way interaction was significant ($F(1,14) = 11.566$; $p < 0.004$), whereas the main effects of day and group were not significant (both $p > 0.5$). Contrary to what we observed in the main experiment, the observers in the DecInc group did not show a lower PSE as testing began on day 2 compared to the IncDec group ($t(14) = 0.323$; $p = 0.751$), possibly indicating that the re-calibration induced without saccades is less stable. Similar to what we had observed in the main experiment, the overall PSE change seems smaller when the observers were exposed to a size increase. This is most likely due to a general bias to report peripheral objects as being smaller (e.g., [4]).

Overall, our results indicate that the visual system continuously keeps size calibrated across the visual field. This complements another learning phenomenon, saccadic adaptation [20], where a trans-saccadic change in position leads to subsequent adjustments in the saccade metrics. This allows the oculomotor system to adapt to fluctuations and changes in the activity of the minutely controlled eye muscles. The specifics differ for saccadic adaptation, which is limited to the motor output and does not lead to a re-calibration of perceived position [21]. Furthermore, it is directionally specific [22, 23], whereas the trans-saccadic re-calibration of size is not bound to the saccade target location. However, both processes together, re-calibration at the motor and sensory side of the action-perception loop, make sure that we always perceive the most-adequate peripheral image and are able to act on it in the proper way.

Whereas our results are largely consistent with the idea that sensorimotor contingencies maintain perceptual uniformity throughout the visual field [1, 3, 5, 6, 24, 25], they notably generalize this notion. We observed re-calibration even if the feedback about the prediction is provided in the absence of eye movements, indicating that predictions based on multiple sources of feedback about the relative appearance of stimuli in central and peripheral viewing are taken into account for re-calibration. Whereas predicting the consequences of our actions is a fundamental aspect of motor control [26–28], predictive mechanisms have a much more widespread role in both perception and

cognition. Arguably, perceiving the world can be seen as the construction of an internal model to predict changes in sensory stimulation due to internally triggered and externally determined events [29–32]. Our results show that prediction errors related to external events are indeed able to modify our perceptual system. The role of trans-saccadic prediction is still fundamental for perceptual re-calibration, because in our everyday life, the most likely reason why a stimulus would end up in central viewing after having been viewed peripherally is that we executed a saccadic eye movement toward it.

We have shown that a continuous process of re-calibration, based mainly on the sensory consequences of our motor actions, underlies our subjective impression of uniformity throughout the visual field. Many objects in the world lead to peripheral images on the retina that cannot be distinguished—so called metamers [33]. We propose that prediction selects the most likely real-world object as our percept, rather than something based on the impoverished eccentric retinal images. Thus, objects in our peripheral visual field do not appear distorted or blurred [34] because our visual system learned to predict a given peripheral visual signal from the corresponding foveal signal. The learning of those peripheral-foveal contingencies is a continuous process that keeps fine-tuning our perceptual system throughout the lifespan.

EXPERIMENTAL PROCEDURES

Methods and procedures were approved by the local ethics committee LEK FB06 at Giessen University (proposal number 2009-0008). Each trial in our main paradigm started with the observers viewing one stimulus in the fovea and one stimulus 20° in the periphery, whose radii varied between trials (Figure 1A; Supplemental Experimental Procedures). The observer was asked to first compare the size of the two stimuli and then to look to the other stimulus and indicate the direction of its protrusion. During the eye movement, depending on the conditions and unnoticed to most observers, the radius of the target stimulus could increase or decrease by up to 10%. A detailed description of the other experiments is available in the Supplemental Experimental Procedures. Psychometric curves were fit to the size comparison responses over partially overlapping intervals of 100 trials, so as to chart the evolution of perceived size, i.e., the PSEs, over the course of the experiment.

REFERENCES

1. O'Regan, J.K., and Noë, A. (2001). A sensorimotor account of vision and visual consciousness. Behav. Brain Sci. *24*, 939–973, discussion 973–1031.

2. Cox, D.D., Meier, P., Oertelt, N., and DiCarlo, J.J. (2005). 'Breaking' position-invariant object recognition. Nat. Neurosci. *8*, 1145–1147.

3. Herwig, A., and Schneider, W.X. (2014). Predicting object features across saccades: evidence from object recognition and visual search. J. Exp. Psychol. Gen. *143*, 1903–1922.

4. Newsome, L.R. (1972). Visual angle and apparent size of objects in peripheral vision. Percept. Psychophys. *12*, 300–304.

5. Herwig, A., Weiss, K., and Schneider, W.X. (2015). When circles become triangular: how transsaccadic predictions shape the perception of shape. Ann. N Y Acad. Sci. *1339*, 97–105.

6. Weiß, K., Schneider, W.X., and Herwig, A. (2014). Associating peripheral and foveal visual input across saccades: a default mode of the human visual system? J. Vis. *14*, 1–15.

7. Deubel, H. (1995). Is saccadic adaptation context-specific? In Eye Movement Research: Mechanisms, Processes, and Application (Studies in Visual Information Processing 6), J.M. Findlay, R. Walker, and R.W. Kentridge, eds. (Elsevier), pp. 177–187.

8. Alahyane, N., and Pélisson, D. (2005). Long-lasting modifications of saccadic eye movements following adaptation induced in the double-step target paradigm. Learn. Mem. *12*, 433–443.

9. Karni, A., and Sagi, D. (1991). Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. Proc. Natl. Acad. Sci. USA *88*, 4966–4970.

10. Hung, S.C., and Seitz, A.R. (2014). Prolonged training at threshold promotes robust retinotopic specificity in perceptual learning. J. Neurosci. *34*, 8423–8431.

11. Xiao, L.Q., Zhang, J.Y., Wang, R., Klein, S.A., Levi, D.M., and Yu, C. (2008). Complete transfer of perceptual learning across retinal locations enabled by double training. Curr. Biol. *18*, 1922–1926.

12. Daniel, P.M., and Whitteridge, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. J. Physiol. *159*, 203–221.

13. Rovamo, J., and Virsu, V. (1979). An estimation and application of the human cortical magnification factor. Exp. Brain Res. *37*, 495–510.

14. Horton, J.C., and Hoyt, W.F. (1991). The representation of the visual field in human striate cortex. A revision of the classic Holmes map. Arch. Ophthalmol. *109*, 816–824.

15. Murray, S.O., Boyaci, H., and Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. Nat. Neurosci. *9*, 429–434.

16. Pooresmaeili, A., Arrighi, R., Biagi, L., and Morrone, M.C. (2013). Blood oxygen level-dependent activation of the primary visual cortex predicts size adaptation illusion. J. Neurosci. *33*, 15999–16008.

17. Schwarzkopf, D.S., Song, C., and Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. Nat. Neurosci. *14*, 28–30.

18. Sperandio, I., Chouinard, P.A., and Goodale, M.A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. Nat. Neurosci. *15*, 540–542.

19. Deubel, H., and Schneider, W.X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res. *36*, 1827–1837.

20. Mclaughlin, S.C. (1967). Parametric adjustment in saccadic eye movements. Percept. Psychophys. *2*, 359–362.

21. Bahcall, D.O., and Kowler, E. (1999). Illusory shifts in visual direction accompany adaptation of saccadic eye movements. Nature *400*, 864–866.

22. Deubel, H., Wolf, W., and Hauske, G. (1986). Adaptive gain control of saccadic eye movements. Hum. Neurobiol. *5*, 245–253.

23. Miller, J.M., Anstis, T., and Templeton, W.B. (1981). Saccadic plasticity: parametric adaptive control by retinal feedback. J. Exp. Psychol. Hum. Percept. Perform. *7*, 356–366.

24. Bompas, A., and O'Regan, J.K. (2006). More evidence for sensorimotor adaptation in color perception. J. Vis. *6*, 145–153.

25. Bompas, A., and O'Regan, J.K. (2006). Evidence for a role of action in colour perception. Perception *35*, 65–78.

26. Wolpert, D.M., Miall, R.C., and Kawato, M. (1998). Internal models in the cerebellum. Trends Cogn. Sci. *2*, 338–347.

27. Wolpert, D.M., and Miall, R.C. (1996). Forward models for physiological motor control. Neural Netw. *9*, 1265–1279.

28. Wolpert, D.M., and Kawato, M. (1998). Multiple paired forward and inverse models for motor control. Neural Netw. *11*, 1317–1329.

29. Bubic, A., von Cramon, D.Y., and Schubotz, R.I. (2010). Prediction, cognition and the brain. Front. Hum. Neurosci. *4*, 25.

30. Yuille, A., and Kersten, D. (2006). Vision as Bayesian inference: analysis by synthesis? Trends Cogn. Sci. *10*, 301–308.

31. Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behav. Brain Sci. *36*, 181–204.

32. Friston, K., and Kiebel, S. (2009). Cortical circuits for perceptual inference. Neural Netw. *22*, 1093–1104.

33. Freeman, J., and Simoncelli, E.P. (2011). Metamers of the ventral stream. Nat. Neurosci. *14*, 1195–1201.

34. Galvin, S.J., O'Shea, R.P., Squire, A.M., and Govan, D.G. (1997). Sharpness overconstancy in peripheral vision. Vision Res. *37*, 2035–2039.