

Shape-specificity of neural persistence for kinetic-depth effect matches perceptual adaptation but not sensory memory

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Abstract

When multistable displays – stimuli that are compatible with several comparably likely perceptual interpretations – are presented intermittently, the perceptual state at the stimulus onset shows a complex dependence on the duration of the preceding blank interval. Specifically, perception is maximally destabilized for interruptions that are approximately 500 ms long, but is stabilized by the use of shorter or longer blank intervals. This non-monotonic dependence of perceptual stability on the blank interval duration raises questions about a number of history effects involved and about their nature, including the underlying neural representations. One way to characterize history effects is by looking at their specificity to the change of display properties. Here, we measured shape-specificity for the perception of kinetic-depth effect when interruptions were brief (50 ms). For this time interval, perception is thought to be stabilized by neural persistence, a lingering trace of the prior neural activity. We found that perceptual stability depended on the shape of objects presented both before and after the break, but not on the similarity between them. These results matched earlier reports on shape-specificity of neural adaptation (destabilizing aftereffect for blanks 200-800 ms long). However, they were markedly different from the shape-specificity of sensory memory of multistable perception (stabilizing effect for blanks >800-1000 ms). We conclude that whereas neural persistence and adaptation both act on the same motion-selective neural representation, sensory memory depends on another, possibly partially overlapping, shape-selective neural ensembles.

Significance

Intermittent presentation of multistable displays reveals a complex non-monotonic relationship between the duration of a blank interval and the stability of perception. We showed that the shape-specificity of neural persistence (stabilizing effect that is evident for short blank intervals < 200 ms) matches that of perceptual adaptation (destabilizing aftereffect for blanks 200-800 ms long) but not of sensory memory of multistable perception (stabilizing effect for blanks > 800-1000 ms). This means that whereas the two former effects can be modeled using the same motion-selective neural ensemble, the latter requires additional shape-selective neural representations.

Introduction

Multistable displays, such as the kinetic-depth effect used in the current study, are compatible with several comparably likely perceptual interpretations. When they are viewed continuously, the observer's perception oscillates between these alternative percepts (Leopold & Logothetis, 1999; Tong, Meng, & Blake, 2006). However, when multistable displays are presented intermittently, their initial perceptual state at the onset of each presentation – sometimes called *percept choice* (Noest, van Ee, Nijs, & van Wezel, 2007) – shows a complex dependence on stimulus properties (Hupé & Rubin, 2003; Song & Yao, 2009), prior perceptual history (Brascamp et al., 2008; Pastukhov & Braun, 2008), and the duration of the blank interval (Klink et al., 2008; Kornmeier & Bach, 2004).

The effect of the blank interval duration follows a non-monotonic inverted U-shape curve (Kornmeier & Bach, 2004) with maximal destabilization occurring, typically, for interruptions that are 400-500 ms long. Both shorter and longer blank intervals lead to a more stable perception. Tentatively, the former stabilization occurs due to neural persistence, a lingering trace of the neural activity, effective for brief interruptions <500 ms (Coltheart, 1980; Loftus & Irwin, 1998), and the latter due to sensory memory of multistable displays, a visual memory specific to multistable displays (de Jong, Knapen, & van Ee, 2012) that biases onset perception towards a recently dominant perceptual state (Leopold, Wilke, Maier, & Logothetis, 2002). However, the two stabilizing effects are sometimes bundled together under the common “priming” label, implying a single stabilizing memory mechanism (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Jiang, Jiang, & Parasuraman, 2014). It has been also suggested that a single neural mechanism can be responsible for all these negative and positive history effects (Brascamp et al., 2007).

One way to understand the history effects at play is by examining whether they depend on and influence the same neural representations. This, in turn, can be deduced by measuring their stimulus-specificity by systematically varying stimuli before and after the interruption and measuring how that changes the effect's strength. For example, this approach was used to characterize the feature-selectivity of sensory memory for binocular rivalry (Pearson & Clifford, 2004). For the kinetic-depth effect (KDE) displays it was used to measure *shape-specificity*, *i.e.*, how the strength of the effect is changed when a specific shape is used (*e.g.*, a sphere or a cylinder) and whether it depends on the difference in the shape of the objects presented before and after interruption (*e.g.*, a sphere followed a cylinder versus a sphere followed by a sphere). It was measured for the perceptual adaptation (Pastukhov, Lissner, & Braun, 2014) and for sensory memory of multistable displays (Pastukhov, Füllekrug, & Braun, 2013). The former is modulated by the shape of the objects and, more specifically, its strength appears to be related to the volume of an object. However, strength of the adaptation does not depend on whether the two objects, presented before and after the interruption, are the same or not. Conversely, sensory memory is modulated by the similarity of two objects and is strongest when the same object is presented before and after the blank. When the two objects are not identical, the strength of sensory memory is proportional to their similarity, which can be defined as an overlap between the two shapes (see figures 6 and 7 in Pastukhov et al., (2013)). However, sensory memory is unaffected by the specific shape(s) of the objects, only by their similarity. Accordingly, this indicates that the two memories influence different, even if potentially overlapping, neural representations.

In the present study, we used this paradigm to investigate the shape-specificity of the history effect for short blank intervals (<200 ms). As noted above, it is thought to occur due to the lingering activation of the neural population after the stimulus offset (Coltheart, 1980; Loftus & Irwin, 1998). This neural persistence enables perception to “bridge” brief interruptions in presentation, integrating sequentially presented stimuli (Eriksen & Collins, 1967). An example of such temporal integration is

binocular rivalry produced by an interleaved dichoptic presentation (O'Shea & Crassini, 1984; van Boxtel, Alais, Erkelens, & van Ee, 2008).

The aim of our work was to characterize the shape-specificity of neural persistence and to compare it to the shape-specificity of the two other history effects, neural adaptation and sensory memory. We report that it matches the former but not the latter.

Methods

Observers





Ten observers (five females), aged 19-42 years participated in this experiment. All procedures were in accordance with the national ethical standards on human experimentation and with the Declaration of Helsinki of 1975, as revised in 2008. The study was in full accordance with the ethical guidelines of the University of Bamberg and was approved by an umbrella evaluation for psychophysical testing of the university ethics committee (Ethikrat) on 18 August 2017. Informed consent was obtained from all observers prior to each experimental session. All participants had normal or corrected-to-normal vision and normal color vision, all tested by standard tests in situ, and were naïve to the purpose of the study. For their participation, observers received credits within the framework of a mandatory module of research participation in accordance with the standards of the University of Bamberg.

Apparatus

Stimuli were generated using custom code and PsychoPy library (Peirce et al., 2019). They were displayed on an EIZO CG245W screen (www.eizoglobal.com/support/db/products/model/CG245W), with the size of the visible area being 52.0 × 32.4 cm operating at a resolution of 1920 × 1200 pixels and a refresh rate of 60 Hz. With a viewing distance of 65 cm, a single pixel subtended 0.023° of visual angle. Participants viewed the display through anaglyph red-green glasses.

The experimental room was dimly lit. Chin and forehead rests were used to stabilize the viewing position. Observers responded using the arrow keys of a computer keyboard.

Stimuli

We employed an ordered “bands” set of four shapes that were used in prior work on shape-specificity of perceptual adaptation (Pastukhov et al., 2014) and sensory memory of multistable displays (Pastukhov et al., 2013), see **Fig. 1A** and the supplementary video. The advantage of this set is that each shape includes shapes to the right (as depicted in **Fig. 1A**). E.g. *dual-band* is a *band* plus an extra band, *quad-band* is a *dual-band* plus two more bands, etc. They also allow for a crude but straightforward measure of shape difference by assigning indices 1 through 4 to, respectively,  *sphere*,  *quad-band*,  *dual-band*, and  *band* and computing the absolute difference between the indices. E.g., *quad-band* is more similar to the *dual-band* than to the *band* stimulus. Note, however, that different dissimilarity levels have different number of corresponding stimuli pairs. Specifically, for the dissimilarity of 1, the results were averaged over three pairs of stimuli; for the dissimilarity of 2, over two pairs; but for the dissimilarity of 3, the data comes from a single pair (a sphere versus a band).

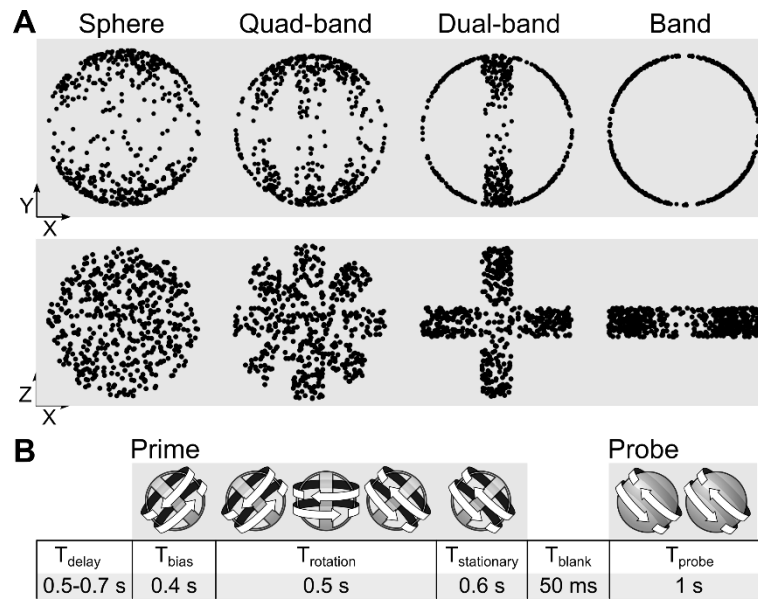


Fig. 1. Displays and procedure. A) Four objects used in the study as viewed on the screen (top row) and from above (bottom row). B) The schematic procedure, time intervals are not drawn to scale. See also the supplementary video. T_{delay} – randomized onset delay at the beginning of each trial. T_{bias} – time interval when stereo disambiguation was applied to bias prime’s direction of rotation. T_{rotation} – time interval when the axis of rotation rotated by 90° to the complementary orientation, in this case from 45° counterclockwise to 45° clockwise. $T_{\text{stationary}}$ – time interval when the prime was fully ambiguous and rotated around the final axis of rotation. T_{probe} – time interval with the probe stimulus.

The kinetic-depth-effect displays stimuli consisted of 2000 dots distributed randomly over the surface of the objects. All shapes were generated anew for each trial. All objects measured 4° in height and rotated at 0.25 Hz. The diameter of the individual dots represented 0.15° and their luminance was 110 cd/m².

Procedure

Each experimental session consisted of eleven experimental blocks. The first block was dedicated to training and was discarded from the analysis. Each block consisted of 48 trials so that each ordered pair of objects was presented four times. Individual trials consisted of the prime period (1500 ms), followed by a brief blank (50 ms), and a probe period (1000 ms), see **Fig. 1B**. Following the presentation, the participants reported on the final direction of rotation of both objects.

The axis of rotation of the prime was initially tilted by 45° either clockwise or counterclockwise, the specific orientation was picked randomly on each trial. The axis of rotation remained stationary for 400 ms before rotating to the opposite complementary orientation, respectively, counterclockwise or clockwise. The rotation of the axis took 500 ms. The orientation of the axis of rotation of the probe matched the final one of the prime. The purpose of this manipulation was to reduce the opposing influence of perceptual adaptation, which would otherwise mask the effect of neural persistence (Blake, Sobel, & Gilroy, 2003).

During the initial 400 ms (T_{bias}), the prime shape was biased towards a random direction of rotation via stereoscopic cues. The projections for the two eyes differed in their orientation around the vertical axis by 0° (fully ambiguous) up to 1° (maximally disambiguated). The disambiguation strength was maximal at the onset and was linearly reduced to zero over the course of 400 ms. The purpose of this manipulation was to randomize the prime’s direction of rotation. Otherwise, the direction of

rotation of both the prime and the probe could be determined by a common perceptual history, making it hard to disentangle the influence of the prime from that of the common effects, such as sensory memory (Leopold et al., 2002).

Statistical analysis

Following (Leopold et al., 2002), the influence of a perceptual state of the prime on that of the probe was quantified using the probability of survival (P_{survival}), which is a probability that both objects rotated in the same direction. Values above 0.5 indicate the stabilizing history effect (probe tends to rotate in the same direction as the prime). Conversely, values below 0.5 indicate destabilizing history effect (probe tends to rotate in the opposite direction).

The analysis was performed in *R* (R Core Team, 2018), version 3.5.1. The effect of prime and probe shapes and their interaction were assessed using linear mixed models (Bates, Mächler, Bolker, & Walker, 2015) with a logit link function. Bayes Factor was computed using the *BayesFactor* package (Morey & Rouder, 2012). The coefficient of determination based on the likelihood-ratio test was computed using the *MuMIn* package (Barton, 2019).

Results

The results of the experiment are summarized in **Fig. 2** and **Table 1**. In short, only the shape of the prime and the probe influenced the strength of the persistence aftereffect, but we observed no interaction between them, indicating that persistence did not depend on the similarity of the two shapes. We also assessed this hypothesis by computing the probability of survival as a function of (dis)similarity of shapes, with a linear mixed model analysis showing no effect (**Fig. 2B**). Moreover, a shape that was a good prime was also a good probe and vice versa, as the probabilities of survival for individual shapes used either as a probe (**Fig. 2C**) or a prime (**Fig. 2D**) were highly correlated ($R=0.97$, $t(38)=23$, $p<.0001$, $BF=3\times 10^{18}$).

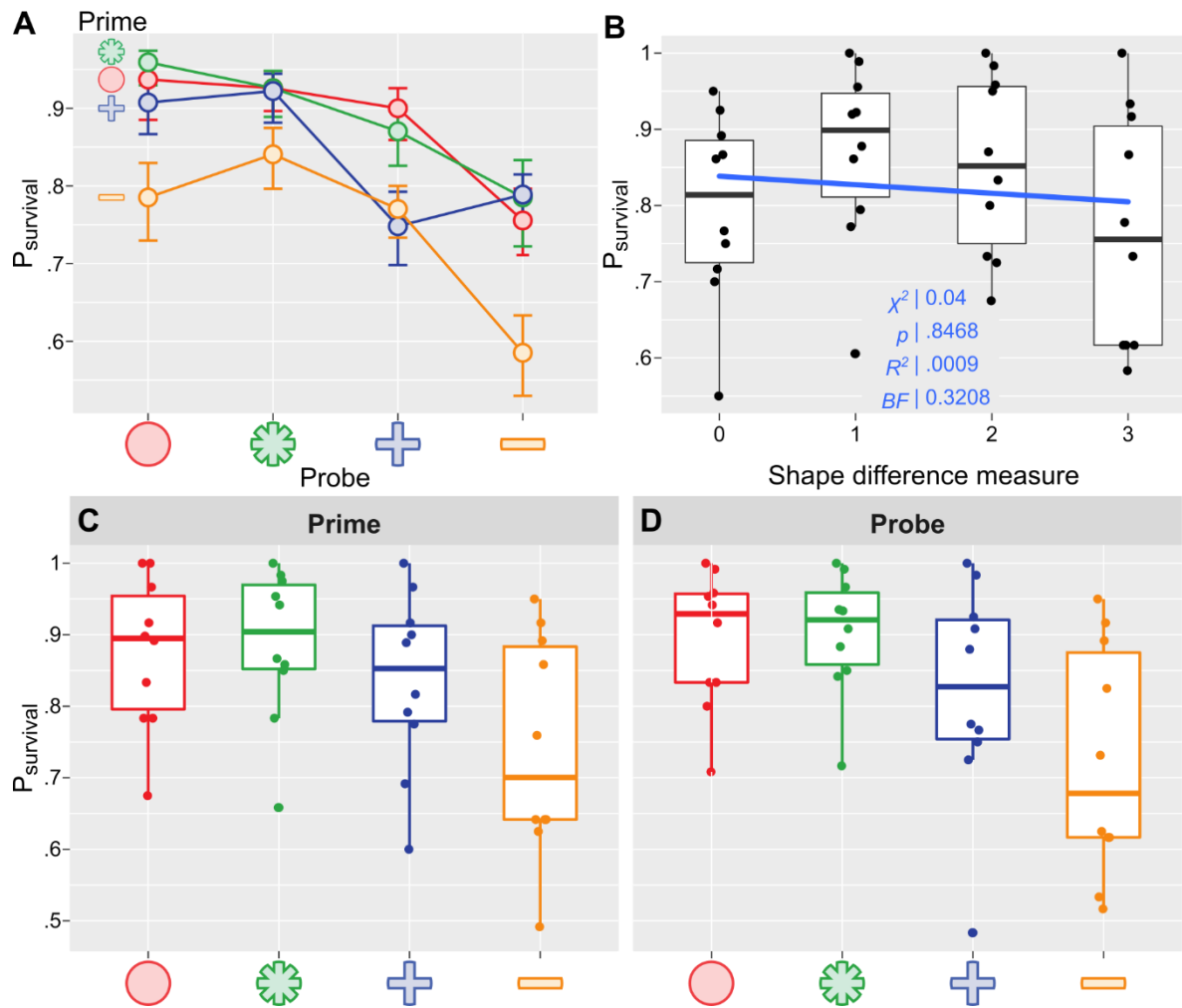


Fig. 2. Results. A) Probability of survival (P_{survival}) as a function of prime (individual lines) and probe (x-axis) shapes. Error bars depict 95% bootstrap bias-corrected accelerated confidence intervals. B) Probability of survival as a function of shape difference between prime and probe shapes (see Methods for details). Dots depict individual participants. The blue line shows a linear regression fit. Inset shows statistics for a linear-mixed model with participants' identity as a random factor and shapes similarity/difference as a fixed factor (R^2 – a coefficient of determination based on the likelihood-ratio test, BF – Bayes Factor, see Methods for details). C, D) Probability of survival for a given shape when it was acting as a prime (C) or a probe (D). Dots depict individual participants.

Table 1. Statistical analysis via hierarchical linear-mixed models with prime and probe shapes as fixed factors and participants' identity as a random factor. *df* – degrees of freedom, AIC - Akaike information criterion, BIC - Bayesian information criterion, logLik – log likelihood, R^2 is a coefficient of determination based on the likelihood-ratio test, BF – Bayes Factor comparing the current model to the previous simpler one.

Model	<i>df</i>	AIC	BIC	logLik	deviance	χ^2	<i>p</i>	R^2	BF
random effects	2	796	802	-396	792				
+ prime	5	791	807	-391	781	10.7	.0132	.06	0.11
+ probe	8	779	804	-382	763	17.7	.0005	.16	3.43
+ prime × probe	17	793	845	-380	759	4.4	.8867	.19	0

Finally, we compared the results of our experiment with two earlier studies of shape-specificity in perceptual adaptation (Pastukhov et al., 2014) and sensory memory (Pastukhov et al., 2013). To this end, we computed the average probability of survival for each pair of shapes (sixteen data points per study) and plotted it against the probability of survival for the same pair of shapes in this study. Our current results were a mirror image of perceptual adaptation (red plot in **Fig. 3**). In other words, pairs of shapes that led to stronger persistence for short blanks (50 ms) also led to stronger adaptation aftereffects for longer blank intervals (~500 ms) or when the neural persistence was curtailed via a mask to maximize the influence of the adaptation (see experiment 2 in Pastukhov et al., (2014)). However, we found no correlation between neural persistence and sensory memory (blue plot in **Fig. 3**). Thus, persistence for short blank intervals (50 ms) did not predict persistence for long blank intervals (1000+ ms).

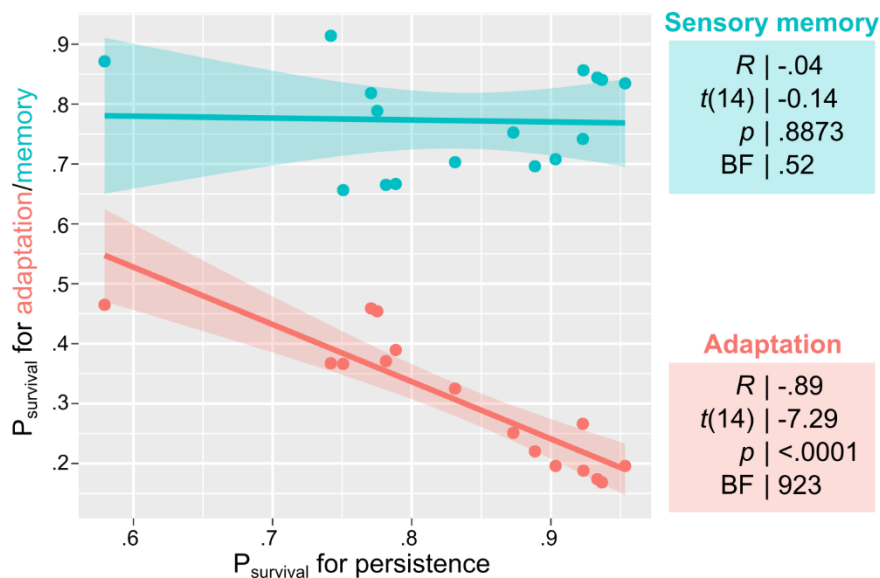


Fig. 3. Comparison with prior work. Probability of survival for neural persistence (x-axis) as compared to that of perceptual adaptation (red plot) and sensory memory (blue plot). Individual dots indicate the average probability of survival for different pairs of shapes. Lines and shaded regions depict fitted linear models and their standard errors. Tables on the right show statistics for Pearson's correlation analysis. BF – Bayes Factor.

Discussion

The aim of this study was to investigate the shape-specificity of neural persistence for kinetic-depth effect displays and to compare it to the shape-specificity of other history effects. We report that the shape of the prime and of the probe objects strongly modulated the probability that the same direction of motion was reported before and after the break. However, we found no interaction between the prime and the probe, with shapes' similarity having no effect on the probability of survival. When comparing the results of the current study with those for perceptual adaptation (Pastukhov et al., 2014) and sensory memory (Pastukhov et al., 2013), we found a strong negative correlation with the former but no correlation with the latter.

As noted in the Results section, the observed probability of survival for individual pairs of shapes is an almost perfect mirror image of the earlier study on the shape-specificity of perceptual adaptation, see **Fig. 3** above and Figure 2 in Pastukhov et al. (2014). In other words, shapes that led to stronger persistence for short blank intervals also produced stronger perceptual adaptation. In both cases, shapes that produced stronger history effects as prime were also more sensitive as probes. Also, in both cases, the effects were stronger for the objects that had bigger "volume", see Figure 7 in Pastukhov et al. (2014). However, further studies are required to clarify the relationship between shape geometry and activation of the underlying neural representations. Taken together, these results indicate that the same or heavily overlapping neural representations are involved in both history effects. This validates earlier experimental and theoretical work suggesting that these two opposing influences can be modeled using a single mechanism (Brascamp et al., 2007).

Conversely, shape-specificity for neural persistence (a positive effect over short blank intervals <200 ms), was markedly different to that of sensory memory of multi-stable displays (also a positive history effect but for longer blanks >1000 ms). Prior evidence shows that their difference goes beyond shape-specificity. For example, neural persistence is sensitive to masking (Irwin & Thomas, 2008), whereas the sensory memory of multistable perception is not (Maier, Wilke, Logothetis, & Leopold, 2003). This indicates that although the two effects may appear to be similar and are even sometimes bundled together under a common "priming" label (Brascamp et al., 2007; Jiang et al., 2014), they rely on different neural mechanisms and should be studied and modeled as two independent effects.

Dependence of sensory memory on an object's shape congruency makes it tempting to view it as a "higher level" memory as compared to neural persistence and perceptual adaptation. However, that may not be the case as other properties of sensory memory indicate its low-level sensory nature. For example, it is maintained independently for individual visual features rather than for an object as a whole (Pearson & Clifford, 2004). It is also specific to a retinotopic location of the original stimulus (Knapen, Brascamp, Adams, & Graf, 2009). These properties are clearly at odds with an idea of a high-level object-based memory and are rather similar to those of neural persistence (McRae, Butler, & Popiel, 1987; Pastukhov, Prasch, & Carbon, 2018) and perceptual adaptation (Clifford et al., 2007). Perhaps, shape-specificity of sensory memory may indicate that it has a special role in perceptual inference (Pastukhov, 2016). However, our current lack of understanding of neural mechanisms and even of the purpose of sensory memory complicates the comparison with the other two history effects.

As noted above, identical shape-specificity of neural persistence and perceptual adaptation indicates that the same neural populations both persist and adapt. Prior neurophysiology (Dodd, Krug, Cumming, & Parker, 2001) and imaging studies (Brouwer & van Ee, 2007) place them in the medial temporal region within the dorsal visual stream, see also (Orban, 2011) for a comprehensive review. In contrast, shape-congruent sensory memory may also involve neurons in neighboring object-

sensitive lateral occipital cortex (Ferber, Humphrey, & Vilis, 2003) or in regions of intraparietal sulcus (Vanduffel et al., 2002).

To conclude, we report that the strength of neural persistence depends only on the shape of the two objects, not on their similarity. This shape-specificity is identical to that of perceptual adaptation but is different from that for the sensory memory of multistable displays. Thus, for ambiguously rotating kinetic-depth effect displays, the same motion-sensitive neurons persist and adapt.

Open Practices Statement

All data files and the analysis code are available under Creative Commons Attribution 4.0 International Public License at <https://osf.io/cdtfr> or at <https://github.com/alexander-pastukhov/shape-specificity-of-neural-persistence>.

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