Report

Current Biology

Opposite Effects of Recent History on Perception and Decision

Highlights

- Recent history induces opposite biases in perception and decision
- Negative adaptation repels perception away from previous stimuli
- Positive serial dependence attracts decisions toward previous decisions
- Serial dependence of perceptual decisions may rely on biases in working memory

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In Brief

Fritsche et al. show that recent history biases perception and post-perceptual decisions in opposite directions. While perception is repelled away, decisions are attracted toward the recent history. These opposite biases may enable an optimal balance between maximizing change sensitivity and maintaining stable representations.

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Opposite Effects of Recent History on Perception and Decision

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SUMMARY

Recent studies claim that visual perception of stimulus features, such as orientation, numerosity, and faces, is systematically biased toward visual input from the immediate past [1–3]. However, the extent to which these positive biases truly reflect changes in perception rather than changes in post-perceptual processes is unclear [4, 5]. In the current study we sought to disentangle perceptual and decisional biases in visual perception. We found that post-perceptual decisions about orientation were indeed systematically *biased toward* previous stimuli and this positive bias did not strongly depend on the spatial location of previous stimuli (replicating previous work [1]). In contrast, observers' perception was *repelled away* from previous stimuli, particularly when previous stimuli were presented at the same spatial location. This repulsive effect resembles the well-known negative tilt-aftereffect in orientation perception [6]. Moreover, we found that the magnitude of the positive decisional bias increased when a longer interval was imposed between perception and decision, suggesting a shift of working memory representations toward the recent history as a source of the decisional bias. We conclude that positive aftereffects on perceptual choice are likely introduced at a post-perceptual stage. Conversely, perception is negatively biased away from recent visual input. We speculate that these opposite effects on perception and post-perceptual decision may derive from the distinct goals of perception and decision-making processes: whereas perception may be optimized for detecting changes in the environment, decision processes may integrate over longer time periods to form stable representations.

RESULTS

Experiment 1: Perceptual Decisions Are Attracted toward Recent Stimuli

Our first aim was to verify whether perceptual decisions are biased toward stimuli that have been recently perceived, as has been described before [1]. To this end, 25 human observers completed a series of trials in which they were presented with randomly oriented Gabor stimuli and subsequently had to report the perceived orientation of each stimulus by adjusting a response bar (Figure 1A). We then analyzed the dependence of the adjustment responses on the stimulus orientation of the previous trial. We found that adjustment responses were indeed systematically attracted toward the stimulus orientation of the previous trial, replicating a previous report [1]. Although the magnitude of this serial dependence effect was smaller than previously reported, it was highly significant ($p < 0.001$, group permutation test, see the Supplemental Experimental Procedures) and the orientation attraction profile had a very similar shape, with the largest attraction occurring when the relative orientation difference between previous and current stimuli measured $\sim 17^\circ$ (Figure 2A). This attractive bias was spatially broadly tuned, such that it was similar in magnitude when the previous stimulus was presented at a different location 10 visual degrees apart, compared to when it was presented at the same location (different location, Figure 2C: max. attraction = 1.17°, $p < 0.01$; same location, Figure 2B: max. attraction = 1.15°, $p < 0.01$; same versus different: $p = 0.47$). Interestingly, next to the attraction of responses toward previous stimuli with similar orientations, we also observed a repulsion effect for stimuli that were more than 60° different ("peripheral bumps" in Figure 2A, $p = 0.048$), which tended to be stronger when stimuli were presented at the same location (same location: $p = 0.018$; different location: $p = 0.693$; same versus different: $p = 0.070$; see the Supplemental Experimental Procedures for details). In summary, the results of experiment 1 show that perceptual decisions, in the form of adjustment responses, are systematically biased toward similar and repelled from strongly different stimuli that were seen several seconds ago.

On the basis of these findings, one might be tempted to conclude that orientation perception is positively biased toward similar visual input from the recent past. This stands in opposition to the well-studied tilt-aftereffect [6–10], for which perceived orientation is negatively biased away from previous visual input. However, in the current experiment, responses probably result from a combination of perceptual and post-perceptual working memory and decision processes. Notably, although an initial decision about stimulus orientation can be made by the time the Gabor stimulus is presented, the final response about stimulus orientation is occurring only ~ 3 s after the offset of the Gabor stimulus. Hence, in order to reproduce the stimulus, participants have to rely on a working memory representation that could also be biased by stimulus history [4, 5]. Further, reproducing a series

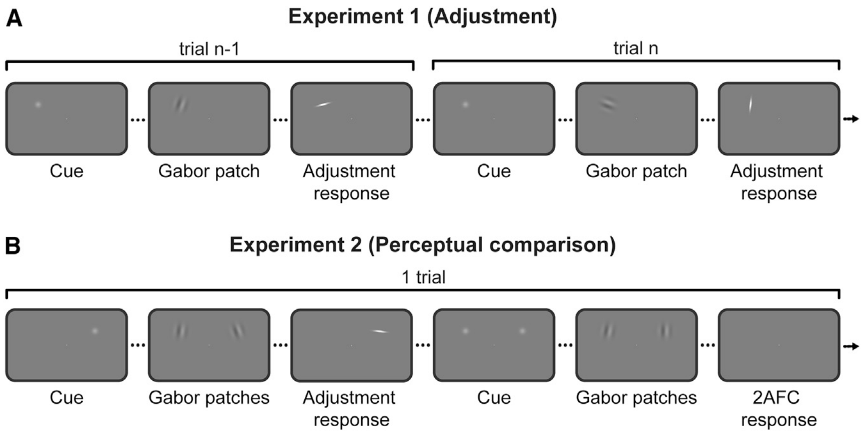

Figure 1. Schematic Sequences of Events in Experiments 1 and 2

(A) Experiment 1. Observers saw a Gabor stimulus at a priorly cued location and subsequently reproduced the orientation of the stimulus by adjusting a response bar. On the next trial, the stimulus was presented either at the same spatial location (as depicted in the figure) or at a different location that was 10 visual degrees above or below the previous stimulus. Stimulus presentation in the left or right visual field alternated between separate, interleaved blocks.

(B) Experiment 2. Observers were cued to reproduce one of two Gabor stimuli by adjusting a response bar (adjustment response). Subsequently, two new Gabor stimuli appeared at priorly cued locations in the left and right visual field. Those stimuli could appear either at the same locations as the previous stimuli or 10 visual degrees above or below. Observers had to judge which of the two new stimuli was oriented more clockwise (2AFC). For detailed illustrations and descriptions of the complete sequences of events within a trial, see Figure S1 and Supplemental Experimental Procedures.

of stimuli with the same type of challenging adjustment response might facilitate carry-over effects on a higher decisional level that is independent of perception. Therefore, it is not clear whether the positive aftereffects measured in adjustment responses occur at a perceptual or a post-perceptual level.

Experiment 2: Repulsive Perceptual Aftereffects during Perceptual Comparison Judgment

In order to study biases of stimulus history on perception in a way that is less vulnerable to post-perceptual processes, a more direct measure of perception is required. One possibility is to measure the appearance of a stimulus in direct comparison to a reference stimulus that is visible at the same time. Such an immediate comparison reduces the potential influence of post-perceptual working memory and decision processes and thus should be systematically biased only if aftereffects caused by previous stimuli alter perception (see experiment 3 in [1] and [4]). Consequently, we used this approach in a second experiment in order to examine the effect of stimulus history on perception, as well as its spatial tuning profile. This experiment was completed by the same set of observers as in experiment 1, allowing us to relate perceptual biases during experiment 2 to decisional biases during experiment 1.

Observers had to perform two consecutive tasks on each trial. First, they were simultaneously presented with two Gabor stimuli and were cued to reproduce the orientation of one of the stimuli by adjusting a response bar. We term the cued stimulus "inducer," since stimulus and task were identical to experiment 1 and induced a perceptual decision at one location. In order to measure subsequent biases on perception, another two Gabor stimuli were presented (one at the previously cued location and one at a location in the opposite hemifield, 20 visual degrees apart) and observers judged which of the two stimuli was tilted more clockwise (two-alternative forced choice [2AFC], Figure 1B). We found that the inducer stimulus systematically biased the perceived orientation of the stimulus that was subsequently presented at the same location. Crucially, however, instead of a bias in perception toward the inducer stimulus, we observed a sizable and highly significant repulsive bias away from the orientation of the inducer (Figure 3A). This negative repulsive effect resembles the well-known tilt-aftereffect in orientation perception [6]. Importantly, the negative aftereffect was markedly reduced when the inducer stimulus was presented at a different spatial location than the subsequently presented stimulus (same location, Figure 3A: $\Delta PSE = -1.40°$, $p < 0.0001$; different location, Figure 3B: $\Delta PSE = -0.42°$, $p = 0.022$; same versus different: $p < 0.001$; group permutation tests, see the Supplemental Experimental Procedures), in line with previous reports outlining the retinal specificity of the tilt-aftereffect [11–13]. Overall, our results show that within the same observers, whose adjustment responses were attracted toward the previous stimulus orientations in experiment 1, perception of stimuli was repelled away from previous stimulus orientations in experiment 2, and this proved to hold even for observers with the strongest positive biases in experiment 1 (see Figure S2). This suggests that the response biases measured in experiment 1 may not be perceptual in nature, but arise at a post-perceptual working memory or decision stage.

Experiment 3: Repulsive Perceptual Aftereffects during Perceptual Equality Judgment

The finding of repulsive perceptual aftereffects in experiment 2 stands in contradiction to results of a previous experiment with identical experimental design and very similar stimulus parameters that reported attractive serial dependence on perception (experiment 3 in [1]). This previous experiment was conducted in a small sample ($n = 3$), precluding strong conclusions (cf. $n = 25$ in current experiment). Nevertheless, we conducted a third experiment with a new set of 24 naive observers, to replicate and extend our findings and to rule out that small differences in experimental design between experiments 1 and 2, over and above the different report methods (adjustment versus perceptual comparison), could have led to opposite effects. Experiment 3 was similar to experiment 2, except for the following modifications. First, stimulus orientations in experiment 1 were drawn from the whole interval of possible orientations, whereas in experiment 2 they were constrained to a range around vertical. Thus, in order to rule out that this difference in across-trial aggregate orientation statistics between experiments caused the opposite effects, stimulus orientations in

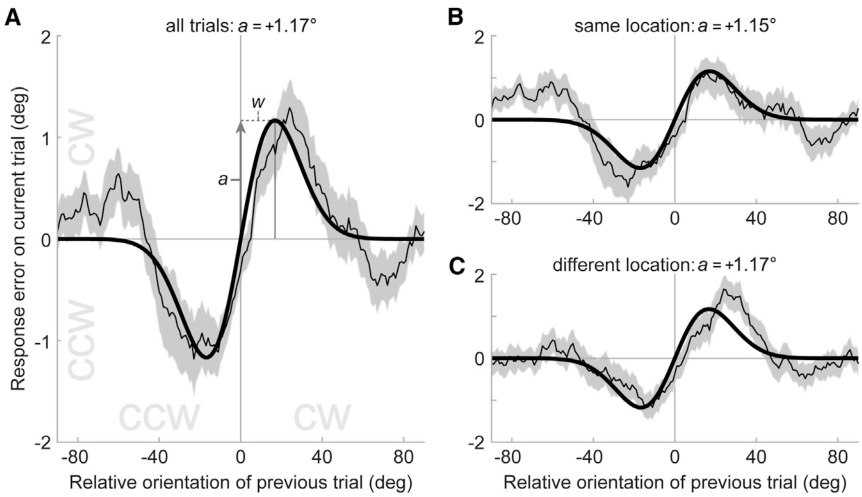

Figure 2. Group Data and Results of Experiment 1: Positive Bias of Responses toward Previous Stimuli Transfers across Spatial Locations

(A) Serial dependence error plot of all trials, irrespective of changes in spatial location. We expressed the response errors (y axis) as a function of the difference between previous and current stimulus orientation (x axis). For positive x values, the previous stimulus was oriented more clockwise than the current stimulus and for positive y values the current response error was in the clockwise direction. Responses are systematically biased toward the previous stimulus, as is revealed by the group moving average of response errors (thin black line). The bias follows a Derivative-of-Gaussian shape (DoG, model fit shown as thick black line). Parameters *a* and *w* determine the height and width of the DoG curve, respectively. Parameter *a* was taken as the strength of serial dependence, as it indicates how much the response to the current stimulus orientation was biased toward a previous stimulus with the maximally effective orientation difference between stimuli. In addition, next to the attraction effect between stimuli with similar orientations, the group data revealed a repulsion effect when current and previous stimuli had very different orientations (difference > 60°), as can be seen at the peripheral regions of the plot. Shaded region depicts the SEM of the group moving average. See also Figure S3.

(B) Serial dependence for "same location" trials. Same plot as in (A), but only considering trials for which the previous stimulus was presented at the same location as the current stimulus.

(C) Serial dependence for "different location" trials. Same plot as in (A), but only considering trials for which the previous and current stimulus location was 10 visual degrees apart.

experiment 3 were randomly drawn from the whole range of possible orientations. Second, inter-stimulus interval timings in experiment 3 were slightly adapted to match them exactly to the timing of experiment 1. Finally, one might be worried that the negative perceptual bias reported in experiment 2 is a result of a response bias due to the comparative 2AFC judgment, and not truly of perceptual nature (e.g., see [14]). Therefore, instead of asking for a clockwise/counterclockwise judgment in the 2AFC phase, in experiment 3 observers had to judge whether the two simultaneously presented Gabor stimuli were of same or different orientation (equality judgment; for detailed methods see Supplemental Experimental Procedures).

Despite similar timing and orientation statistics, and using a perceptual equality judgment instead of a comparative judgment, we found a highly significant negative aftereffect on orientation perception, which was virtually identical in magnitude to our previous finding (Figure 3C: ΔPSE = $-1.39°$, $p < 0.0001$). Additionally, the current experiment also allowed us to systematically investigate the influence of the previous trial's stimuli on the adjustment response on the current trial. We found a robust attraction of adjustment responses toward the inducer stimulus on the previous trial ($p < 0.001$). Again, this attraction effect was spatially broadly tuned and transferred between subsequent inducer stimuli presented 20 visual degrees apart (Figure S3A; same location: max. attraction = 1.27°, $p < 0.01$; different location: max. attraction = 1.25°, $p = 0.029$; same versus different: $p = 0.47$). Crucially, no such influence was exerted by the temporally closer 2AFC stimuli of the previous trial (Figure S3B; same location: max. attraction = $-0.17°$, $p = 0.43$; different location: max. attraction = 0.35°, $p = 0.28$; same versus different: $p = 0.2$), suggesting that the positive decisional bias is driven by previous perceptual decisions about overall orientation, rather than the previous stimuli as such. Together, these findings demonstrate that decisions about inducer stimuli attract subsequent similar decisions, although they exert a repulsive effect on the *perception* of intervening stimuli. Therefore, these findings add strong support for the hypothesis that perception and post-perceptual decisions are concurrently biased into opposite directions.

Experiment 4: Positive Decision Bias Grows during Post-Perceptual Period

Although our previous experiments suggest that the positive bias arises at a post-perceptual stage of the decision-making process, the specific nature of the bias is not elucidated by these experiments. One possibility is that the working memory representation of the current stimulus is biased toward previous perceptual decisions. This idea is supported by the fact that, in contrast to experiments 2 and 3, in experiment 1 observers had to reproduce each stimulus on the basis of a memory representation. Indeed, previous studies reported trial-to-trial carry-over effects in short-term memory [4, 5]. Consequently, making decisions about perceptual experiences (e.g., the percept of the current stimulus) on the basis of a biased working memory representation of those experiences could lead to a positive bias. One prediction of this view is that the positive bias may be stronger if information about the current stimulus has to be retained in working memory for a longer duration before it is reproduced, effectively granting more time for the working memory representation to be biased. In order to test this prediction, we asked 25 new observers to complete a series of trials in which they had to reproduce the orientations of randomly oriented Gabor stimuli via an adjustment procedure, similar to experiment 1. Crucially, on half of the trials participants could start the

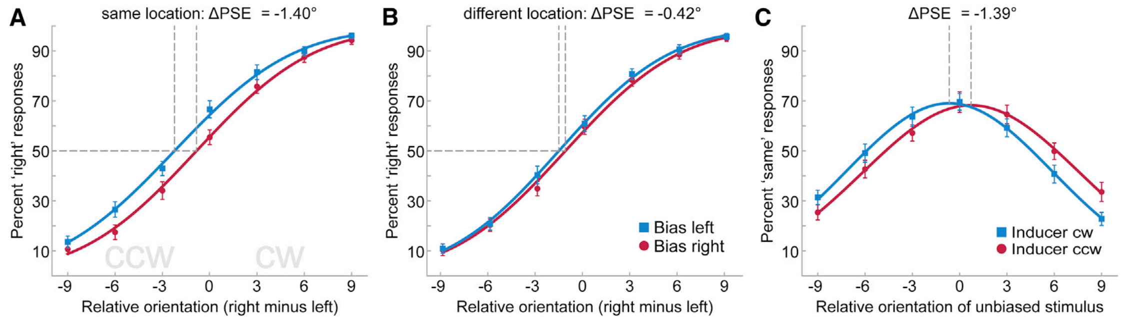

Figure 3. Results of Experiments 2 and 3: Repulsive Bias of Perception away from Previous Stimuli Is Spatially Specific and Does Not Depend on Judgment Method

(A) Psychometric curves for the comparative 2AFC judgment in experiment 2, when the inducer stimulus was presented at the same location as the subsequent 2AFC stimulus. Observers had to indicate which of the two simultaneously presented 2AFC stimuli was oriented more clockwise. We expressed the probability of a "right" response (y axis) as a function of the orientation difference between right and left 2AFC stimuli (x axis). For positive x values, the right stimulus was oriented more clockwise. We binned the trials in two bins according to the expected influence of the inducer stimulus. Red data points represent trials in which a *positive* bias of the inducer would favor a "right" response, while blue data points represent trials in which it would favor a "left" response. As can be seen from the psychometric model fits (blue and red lines), the result is opposite from what would be expected under a positive bias. In other words, perception is *negatively* biased away from the previous stimulus ($p < 0.0001$). The magnitude of the negative bias did not depend on the strength of positive decisional biases measured in experiment 1 (see Figure S2).

(B) Same plot as in (A) but the locations of inducer and subsequent 2AFC stimulus were 10 visual degrees apart. The negative bias was greatly reduced (same versus different location: $p < 0.001$) but still significant ($p = 0.022$).

(C) Results for the equality judgment in experiment 3. Observers had to indicate whether the two simultaneously presented 2AFC stimuli had the same or a different orientation. We expressed the probability of a "same" response (y axis) as a function of the relative orientation of the 2AFC stimulus, which appeared in the opposite hemifield of the inducer stimulus (*unbiased* stimulus) with respect to the orientation of the 2AFC stimulus, presented at the same location as the inducer stimulus (*biased* stimulus). For positive x values, the unbiased stimulus was oriented more clockwise. Red data points represent trials in which the inducer stimulus was oriented counterclockwise with respect to the biased 2AFC stimulus, while blue data points likewise indicate a clockwise tilt of the inducer. As can be seen from the Gaussian model fits (blue and red lines), the unbiased stimulus had to be tilted in the *opposite* direction of the inducer tilt, in order for observers to perceive the 2AFC stimulus orientations as equal ($p < 0.0001$). This repulsive perceptual aftereffect was nearly identical in magnitude to that found in experiment 2.

All data points represent group means and error bars depict SEMs.

adjustment response 300 ms after stimulus offset, whereas on the other half of the trials (pseudo-randomly interleaved), the start of the adjustment response was delayed by 3,750 ms (for detailed methods see Supplemental Experimental Procedures and Figure S4). In line with our prediction, we found that the positive bias considerably increased in magnitude with increasing response delay on the current trial (Figure 4; short delay: max. attraction = 1.08°, $p < 0.001$; long delay: max. attraction = 1.64°, $p < 0.0001$; short versus long: $p = 0.0235$). This suggests that the post-perceptual decision bias occurs due to a shift of the working memory representation of the current stimulus toward recent perceptual decisions. Moreover, this finding provides additional evidence against a perceptual account of the positive bias. In particular, the manipulation of the response delay could not have influenced the way observers perceived the stimulus, as everything was equal up to the point where the stimulus was perceived. Therefore, our finding of a change in bias due to a post-perceptual manipulation renders a perceptual interpretation of the effect unlikely.

DISCUSSION

In a set of four psychophysical experiments, we show that recent history biases perception and post-perceptual decisions in opposite directions. In experiments 2 and 3, which measure the appearance of visual stimuli, we found that perception was *repelled away* from previous stimuli. In contrast, experiments 1 and 4 revealed that post-perceptual decisions in the same observers were *attracted toward* previous stimuli. Moreover, in experiment 4 we showed that the positive attraction effect increased during the post-perceptual retention period, suggesting dynamic biases in working memory as a potential underlying source of the decisional bias. Further, our experiments demonstrate different spatial tuning profiles of the opposite biases: while negative perceptual dependencies are marked by a high spatial specificity, positive post-perceptual dependencies pool over a very broad range of spatial locations. This novel dissociation of serial dependencies in perception and decision stands in opposition to previous reports of positive perceptual serial dependence [1–3, 15, 16] and highlights the importance of studying effects of sensory history on perceptual and post-perceptual processes in separation.

Negative Bias on Perception

The negative perceptual bias in experiments 2 and 3 was spatially specific and resembles the well-studied negative tilt-aftereffect in orientation perception [6–13], which is part of a larger family of negative adaptation effects [17–21]. It is widely assumed that adaptation serves to optimize visual processing [22–24] and maximizes sensitivity to change in the adapted feature dimension [25–27]. Therefore, we speculate that the adaptation effect reported in the current study might be a consequence of one important goal of the visual system, namely to maximize sensitivity to changes in the physical environment.

The presence of adaptation effects in the current experiments might be surprising, as stimuli were presented only briefly, had a

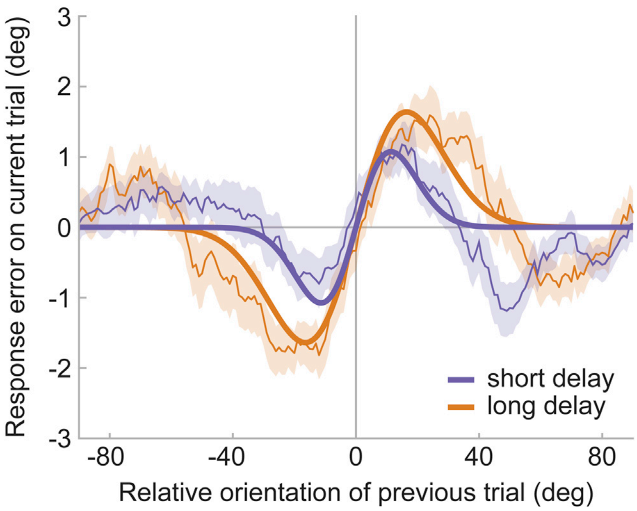

Figure 4. Results of Experiment 4: Positive Decisional Bias Increases when a Longer Delay Is Imposed between Stimulus Presentation and Reproduction

Similar serial dependence error plot as in Figure 2. We separately considered trials in which participants could give the adjustment response shortly after stimulus offset (purple lines) or only after a longer delay (orange lines). As revealed by the group moving averages of response errors (thin lines) and the respective DoG model fits (thick lines), responses were more strongly attracted to the previous stimulus orientation on trials with a longer delay between stimulus presentations and subsequent adjustment responses. Shaded regions depict the SEMs of the group moving averages. For detailed task description, see Supplemental Experimental Procedures and Figure S4.

relatively low contrast, and were backward masked by noise patches. Nevertheless, adaptation was still observable after a period of ~5 s. Although adaptation effects to low-contrast, sub-second stimulation have been previously reported [23, 28], adaptation usually decays very rapidly [29–31]. However, it is plausible that not the previous stimulus itself, but rather a memory trace of the previous stimulus lingering in visual short-term memory is the cause of the five-seconds-long adaptation reported in the current study [32, 33].

Positive Bias on Post-Perceptual Decision

In opposition, the post-perceptual bias measured in adjustment responses attracted decisions toward previous stimuli. Interestingly, in experiment 3 the attraction effect on adjustment responses was present only when observers made a perceptual decision about the overall stimulus orientation on the previous trial (adjustment response), but not when the previous stimuli were judged in terms of their relative orientation difference (equality judgment). This reliance on the particular decision about the previous stimulus renders it likely that not the previous stimulus itself but rather the previous perceptual decision caused the decisional bias on the next trial. Moreover, we found evidence that the decisional bias likely results from a post-perceptual shift of working memory representations of the current stimulus toward previous perceptual decisions, in line with previous reports of trial-to-trial carryover effects in short-term memory [4, 5]. Whether working memory is the only source of this bias, or whether other higher-level phenomena, such as decision inertia [34] or self-suggestion processes, contribute to this bias is an exciting question for future research.

Interestingly, next to positive biases of adjustment responses toward previous stimuli with similar orientations, we also observed negative biases when visual input changed drastically. In other words, when there was a large difference between adjacent stimuli, adjustment responses were repelled away from previous stimuli. Whether these repulsive effects are of perceptual or decisional nature remains to be tested in future experiments.

Concurrently to adaptation effects in perception, the positive biases on post-perceptual working memory content and decisions might serve an important, yet distinct, functional role. Although it is vital to remain sensitive to changes in the immediate present, the physical environment does usually not change drastically over short timescales [35]. Consequently, biasing working memory representations and thus perceptual decisions toward similar recent decisions would make those more robust to random fluctuations that do not reflect actual changes in the external environment.

While the functional distinction between positive and negative biases remains speculative at the moment, a variety of interesting questions arises. For instance, it will be interesting to investigate how the temporal tuning profiles between positive decisional and negative perceptual biases compare. Moreover, it will be important to further elucidate which aspects of the recent history, such as previous stimuli or decisions, contribute to perceptual and decisional biases, respectively. Additionally, it remains to be tested whether and how the opposite biases develop for different settings of stimulus parameters, i.e., contrast, stimulus duration, and additional noise. Finally, it will be vital to elucidate the neural mechanisms that underlie these perceptual and decisional biases [36]. Recently, it has been demonstrated that repulsive adaptation and attractive hysteresis processes map onto distinct higher-order fronto-parietal and early visual cortical networks, respectively [37]. Previously summarized as perceptual effects, it will be crucial to test the nature of those processes more stringently, as advocated in the current study.

Conclusions

Our results demonstrate opposite biases of the recent history on perception and post-perceptual decision processes. While perception is repelled away, post-perceptual decisions are attracted toward the recent history. Therefore, the current study highlights the importance of carefully dissociating between perceptual and post-perceptual effects of temporal context. We speculate that the opposite biases on perceptual and post-perceptual processes may imbue the nervous system with an optimal balance between sensitivity and stability that is required to operate successfully in the environment.

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2017.01.006.

AUTHOR CONTRIBUTIONS

Conceptualization, M.F., P.M., and F.P.d.L.; Methodology, M.F. and F.P.d.L.; Formal Analysis, M.F.; Investigation, M.F.; Writing – Original Draft, M.F. and

F.P.d.L.; Writing – Review & Editing, M.F., P.M., and F.P.d.L.; Funding Acquisition, F.P.d.L.

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