Two primes priming: Does feature integration occur before response activation?

Julianne E. Grainger  
Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique, Fédérale de Lausanne (EPFL), Switzerland

Frank Scharnowski  
Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique, Fédérale de Lausanne (EPFL), Switzerland

Thomas Schmidt  
Faculty of Social Sciences, Psychology I, University of Kaiserslautern, Germany

Michael H. Herzog  
Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique, Fédérale de Lausanne (EPFL), Switzerland

Responses to a target can be sped up or slowed down by a congruent or incongruent prime, respectively. Even though presentations are rapid, the prime and the target are thought to activate motor responses in strict sequence, with prime activation preceding target activation. In feature fusion, the opposite seems to be the case. For example, a vernier offset to the left is immediately followed by a vernier offset to the right at the same location. The two verniers are not perceived as two elements in sequence but as a single, aligned vernier. Here, we ask the question as to how features are integrated: before or after motor activation? We presented two vernier primes with opposite offset directions preceding a single vernier target. No priming effect occurred when the vernier primes were presented at the same location, indicating that verniers integrate before motor activation. There was also no priming effect when the primes were presented simultaneously at different locations, indicating that there is an integration stage different from the perceptual fusion stage. When the second prime is delayed, it determines priming, even for very long delays. To explain these long integration times, we argue that there is a buffer preceding motor activation.

Introduction

The time course of response activation can be examined by response priming (Klotz & Neumann, 1999; Klotz & Wolff, 1995). In response priming, participants perform a speeded response to a target, which is preceded by a prime. The prime is assigned either to the same response as the target (congruent prime) or to the opposite response (incongruent prime). Response priming occurs because primes (pre)-activate a response before the target (e.g., Brenner & Smeets, 2004; Eimer & Schlaghecken, 1998; Leuthold & Kopp, 1998; Song & Nakayama, 2009). Congruent primes speed up responses because the primes preactivate the same response as the target. Likewise, incongruent primes slow responses down. Priming effects increase with ISI because the prime has progressively more time to activate a response, even to the point at which an incongruent prime provokes a full-fledged response error. Consequently, response errors occur almost exclusively in incongruent trials and increase in frequency with increasing interstimulus interval (ISI) (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003).

In kinematic paradigms, the dynamics of response priming can be tracked in great detail. In these experiments, observers point with one index finger to either one of two areas on a tablet. In incongruent trials, the finger first moves to the area assigned to the prime and then changes directions toward the target’s area. In congruent trials, the finger moves on a straight trajectory directly to one point and, thus, responses are much faster than in incongruent trials (Schmidt, 2002; Schmidt & Schmidt, 2009).

In addition, the kinematic studies have shown that the initial response of the motor system to the prime depends only on properties of the prime and is independent of any properties of the target, strongly suggesting that prime and target signals are processed in strict sequence without any mixing or overlapping (Schmidt, Niehaus, & Nagel, 2006; Schmidt & Schmidt, 2009; Vath & Schmidt, 2007). Sequential response activation is well modeled by diffusion processes. For example, Vorberg et al. (2003) used a simple winnertakes-all model in which two leaky accumulators gather sensory evidence for one or the other motor response. In this model, contrary to independent race models, the second prime dominates the priming effect because it replaces the first prime in the response activation process and then has more time to bias motor activation in “its” direction.

Strikingly, response priming can occur without visual awareness of the prime, and the two variables can even have contradictory time courses (Albrecht, Klapötke, & Mattler, 2010; Klotz & Wolff, 1995; Mattler, 2003; Vorberg et al., 2003). With weak assumptions, such double dissociations indicate that response priming and awareness of the prime are based on distinct processes (Schmidt & Vorberg, 2006).

As mentioned, in response priming, prime and target stimuli activate motor responses in strict sequence. The converse seems to occur in feature fusion, where two stimuli are presented in rapid succession and only one single stimulus is perceived. For example, a red disk followed by a green disk is perceived as a yellow disk (Efron, 1967, 1973). Likewise, a right-offset vernier stimulus followed by a left-offset vernier is perceived as a single, almost straight vernier. Interestingly, in feature fusion, the second stimulus dominates perception. In the above examples, the yellow disk appears slightly greenish (Efron, 1967, 1973) and the fused vernier as slightly offset to the left (Herzog, Parish, Koch, & Fahle, 2003). Dominance of the second vernier increases when the duration of both verniers increases (Scharnowski, Hermens, & Herzog, 2007).

In the following, we will distinguish two related processes: feature integration and feature fusion. In a broad sense, integration describes any process in which two stimuli have a combined impact on information processing instead of separate impacts. The term fusion is reserved for the special case in which two stimuli are combined into one single conscious percept. Hence, it is conceivable that two stimuli fuse in conscious perception but do not integrate in response priming, and vice versa.

Here, we address the question as to how feature fusion, feature integration, and response activation are related. First, we wanted to know whether integration of two vernier primes occurs before or after they activate a motor response (Experiment 1). Second, we take a look at the temporal parameters that lead to visuomotor integration when perceptual fusion is precluded (Experiments 2 and 3).

**General materials and methods**

**Participants**

All participants, excluding the participating author, were paid 20 CHF per hour and were informed that they could leave the experiment at any time they wished (none did). All participants had normal or corrected-to-normal vision with a visual acuity greater than 1.0 in at least one eye according to the Freiburg visual acuity test (Bach, 1996). Over all experiments, two participants (not included above) were excluded due to a failure to follow directions.

**Apparatus and stimuli**

Stimuli appeared on a Tektronix 608 X-Y display with a P11 phosphor controlled by a PC using fast 16-bit DA converters (refresh rate of 200 Hz). Stimuli were composed of dots drawn with a dot pitch of 200 μm and a dot rate of 1 MHz. The luminance of the stimuli was 80 cd/m² measured with a Minolta LS-100 luminance meter. Observation distance was 2 m.

None, one, or two vernier primes were presented followed by a variable ISI and then a target vernier (Figure 1a, b shows two examples with two primes). Verniers consisted of two vertical lines, which were offset in the horizontal direction either to the left or right. Vernier primes were 10 arcmin in length (plus a 1 arcmin gap) with offsets of 0.66 arcmin, except in Experiment 1, in which offsets were adjusted individually. The target vernier was 20 arcmin in length (plus a 1 arcmin gap), with offsets of 2.5 arcmin. Primes were presented for 20 ms each.

Participants indicated the offset direction of the target vernier as quickly and accurately as possible by pressing either a left (for a left offset of the lower line) or a right (for a right offset) button. The target was presented for 1 s or until participants gave a response. The large offset size of the target yielded performance levels close to 100%.

**Data analysis**

Priming effects were determined by subtracting response times in congruent trials from those in
incongruent trials for each ISI. The ISI was defined as the time between the offset of Prime 2 and the onset of the target. For statistical analysis, regression lines were fit to the priming effects and subjected to a one-sample, two-tailed t test (Experiments 1 and 2).

In all experiments, reaction times outside of three standard deviations were not included in the data analysis. For the figures, within-subjects error bars were calculated as outlined by Cousineau (2005). For the error rates, a two-tailed, repeated-measures analysis of variance (ANOVA) with factors of ISI and Congruency was performed for each condition individually between the arcsine transforms of the congruent and incongruent error rates (Experiments 1 and 2).

Results

Experiment 1: Feature fusion

In the first experiment, we combined feature fusion with a response priming paradigm; that is, two vernier primes with opposite offsets were followed by a target vernier. Participants indicated the offset direction of the target.

Methods

Five naïve observers and one of the authors took part in this experiment (three women).

One, two, or no prime vernier(s) were followed by a variable ISI and the target vernier. Observers were asked to report the offset direction of the target vernier as quickly and as accurately as possible.

Primes were presented in the center of the screen. When two primes were shown, they were presented in immediate succession in order to create fusion. The target was presented 20 arcmin to the right of the center.

For the two-prime condition, the primes are referred to as Prime 1 and Prime 2 for the first and second prime, respectively. The offset of Prime 1 was chosen randomly in each trial. The offset of Prime 2 was always in the opposite direction.

Previous experiments on feature fusion have found that the second element dominates the fused percept (Efron, 1967, 1973; Herzog et al., 2003). To achieve a balanced fused percept, the Prime 1 offset was fixed at 0.66 arcmin, whereas the Prime 2 offset was adjusted individually so that on average, neither prime dominated the percept. To adjust Prime 2, participants completed 80 trials of the two-prime sequence without the target and reported the offset direction of the fused vernier. If subjects responded above 50% in accordance with Prime 1, then the offset of Prime 2 was increased, or vice versa. The offset of Prime 2 was adjusted until participants responded with 45% to 55% in accordance with the offset direction of Prime 1. On average, Prime 2 was adjusted to an offset size of 0.5 arcmin, in accordance with previous studies (Herzog et al., 2003; Scharnowski et al., 2007; Scharnowski et al., 2009). Participants were not told there were two verniers, and when questioned at the end of the experiment, they reported being unaware of that fact.
Participants completed 12 blocks of 100 trials for each condition. ISIs and congruent versus incongruent primes were presented randomly within blocks. The blocks were completed in random order. Blocks were separated by an optional pause.

**Results**

In the one-prime condition, responses were faster for congruent trials than for incongruent trials, leading to a positive priming effect in accordance with previous studies on response priming \((p < 0.0001; \text{Figure 2a})\). The priming effect increased with ISI. In contrast, no such priming effect was apparent in the two-prime condition \((p = 0.087)\).

In the one-prime condition, reactions were much faster in congruent than in incongruent trials, whereas they are virtually identical in the two-prime condition (Figure 2b). Reaction times decreased also in the no-prime condition. We attribute this effect to an unspecified main effect of ISI. For long ISIs, observers know that the target must appear soon, and hence, responses are faster.

For the error rates, the one-prime condition showed a significant difference between the congruent and incongruent error rates, whereas the two-prime condition did not \((p < 0.04 \text{ and } p = 0.93, \text{respectively}; \text{Figure 2c})\).

**Discussion**

We presented the second vernier with a smaller offset than the first one, such that both verniers were equally contributing to feature fusion. Feature fusion is about conscious vision, in which both verniers and their offsets are integrated into one conscious element in a time-consuming fashion. In general, it is often thought that conscious perception is rather slow and occurs by recurrent processing. Response priming, on the other hand, is thought to occur rather rapidly in a feed-
forward manner, where primes activate motor responses in strict sequence of their presentation. Given that the verniers fuse in conscious vision, do they integrate before or after response activation? If the vernier primes integrate before response activation, no priming effect is expected to occur because the integrated stimulus representation is aligned. In contrast, if primes in the two-prime condition are still able to activate two opposite responses in sequence (first the one assigned to Prime 1, then the one assigned to Prime 2), priming should be observed. Because Prime 2 would have relatively more time to activate its associated response (compared with only 20 ms for Prime 1), we would expect Prime 2 to dominate the priming effect and its sign to be negative. In addition, at very short stimulus onset asynchronies (SOAs), it is possible that the first prime dominates priming because it activates motor responses before the second vernier can counteract its effect.

However, we found no evidence for sequential response activation at all. Except potentially for the shortest ISI, there was no significant priming effect. It seems that the opposite-offset primes fully integrate before activating the motor response, just as they fuse to a single percept in conscious vision.

We know that such fusion occurs when the prime sequence is presented without the target because participants cannot report whether the first or second vernier is offset (Scharnowski et al., 2009).

**Experiment 2: Feature integration**

In the previous experiment, we found that two sequential vernier primes did not lead to response priming. One explanation is that primes integrated to a single, aligned vernier representation before activating the motor response, just like the verniers fuse to an aligned offset in conscious perception. Alternatively, priming may be based on the fused, conscious percept itself. To study whether integration in the visuomotor system can occur in the absence of perceptual fusion, we presented the verniers at different locations, preventing fusion.
Methods

Five naïve observers and one of the authors took part in this experiment (four women). One or two primes were presented before the target vernier, which was presented in the center of the screen. Observers were asked to report the offset of the target vernier as quickly and as accurately as possible. Primes were presented 20 arcmin away from the target.

In the one-prime condition, the prime appeared randomly either on the right or left side of the target.

In the various two-prime conditions, one prime appeared on the left side of the target, the other one on the right side. There were three such conditions:

In the same-time, same-offset condition, both primes had the same offset size and direction.

In the same-time, different-offset condition, both primes had the same offset size but opposite offset directions. In both conditions, the prime on the right-hand side was arbitrarily taken as a reference for congruency. Hence, if this prime was in the same direction as the target, then this was a congruent trial.

Finally, in the different-times condition, the two primes were separated by a 30-ms interval. The prime presented first, independent of whether it was presented on the left or right side, was taken as a reference for congruency.

Participants completed 12 blocks of 100 trials for each condition. ISIs and congruent versus incongruent primes were presented randomly within blocks.

Results

The priming effect increased with increasing ISI for the one-prime and the same-time, same-offset conditions ($p < 0.003$ $p < 0.02$, respectively; Figure 3a). Priming effects had a negative sign in the different-times condition, indicating that Prime 2 dominated ($p < 0.005$). No priming was observed in the same-time, opposite-offset condition ($p = 0.42$).

Whereas there is only a small difference in the priming effect for the one-prime and the same-time, same-offset conditions, mean reaction times are clearly faster in the latter condition. This redundancy gain indicates that both primes were integrated, thus speeding up responses (Figure 3b). Reactions are much faster in the same-time, same-offset, congruent condition than in the same-time, opposite-offset conditions. This result makes sense because, as we argue, both vernier prime offsets are integrated. However, we had expected slower reaction times in the incongruent case than in the same-time opposite-offset condition because two primes are incongruent to the target in the first condition as opposed to only one in the latter condition. In addition, we might have expected reaction times to increase strongly in both conditions, which is, however, not the case. As mentioned before, there is a main effect of ISI on reaction times. However, this can only partially explain these results.

All conditions showed a significant difference between the congruent and incongruent error rates ($p < 0.03$, $p < 0.04$, $p < 0.006$, and $p < 0.05$ for the one-prime, different-times, same-time same-offset, and same-time opposite-offset conditions; Figure 3c).

We like to mention that the long target duration strongly reduced prime visibility, comparable to other masking situations (Breitmeyer & Ögmen, 2006).

Discussion

There are two main results. First, vernier primes are integrated even when presented at different locations. If primes have the same offset direction and are presented simultaneously, responses are faster in congruent compared with incongruent trials (Figure 3b). Opposite offsets seem to cancel each other, as in Experiment 1. The second main result is that when primes are presented one after the other, the second vernier dominates priming. However, this effect occurs only for ISIs of 100 ms and longer.

The results cannot easily be explained by most models of priming. Independent race models assume that both vernier offsets are processed independently and activate motor responses independently. In these models, the first prime dominates priming because evidence accumulation for Prime 1 proceeds for a longer duration than for Prime 2. However, there is no evidence for such independent race models in our experiments. Diffusion models (e.g., Vorberg et al., 2003) propose that primes are not processed independently and that, for long ISIs, the second prime overrides activity of Prime 1 and biases the response toward its offset. Our data favor such diffusion models in principle. However, these models cannot predict that priming is limited to very long ISIs. In the discussion, we will propose that prime features are integrated in a buffer preceding motor activation.

Experiment 3: The time course of integration

In Experiment 3, we varied the ISI between primes. We will show that primes cancel each other even for ISIs between primes as long as 100 ms. This result shows further evidence for a long-lasting buffer.

Methods

Experiment 3 had four naïve participants (two women). Two prime verniers were followed by the target vernier. The interval between the primes was varied. In keeping with the previous experiments, the ISI is also here defined as the time between termination
of Prime 2 and the onset of the target. Two conditions were used: the different-times condition and the varying-prime condition (Figure 4a). In the different-times condition, identical to the condition in Experiment 2, the interval between the two primes was 30 ms and the ISI was varied between 30 and 200 ms. In the varying-prime condition, the time between Prime 1 and the target was kept constant at 200 ms, whereas the timing of the onset of Prime 2 varied throughout this 200-ms interval. Therefore, by changing the timing of the onset of Prime 2, both the ISI and the interprime interval were varied. Importantly, as ISI increases, the interprime interval decreases, such that ISIs of 180, 150, 100, and 30 ms correspond to interprime intervals of 0, 30, 80, and 150 ms.

In each trial, two primes with opposite offsets were presented 20 arcmin to the right and left of the screen center, respectively. The target vernier was presented in the center of the screen and was either congruent or incongruent with Prime 1 as defined in the previous experiments.

Participants completed six blocks of 200 trials. Each block consisted solely of trials from one condition. The side Prime 1 was presented on and the ISI were randomized. The blocks for each condition were completed in random order. Within each block, there were equal numbers of trials from each of the five ISIs. Blocks were separated by an optional pause.

Results

A one-sample, two-tailed t test was performed for each ISI. In the different-times condition, results are similar to those from Experiment 2 (Figure 4b). As predicted, Prime 2 dominates the priming effect at long ISIs, leading to a priming effect of negative sign comparable in size to Experiment 2. Significant priming effects were found only for ISIs of 150 ms and 200 ms, indicating that it takes substantial time before Prime 2 dominates over Prime 1 ($p < 0.004, p < 0.02$ for ISIs of 150 and 200 ms).

In the varying-prime condition, there were no significant priming effects ($p > 0.4, p > 0.08, p > 0.1, p$...
A two-way repeated-measures ANOVA comparing
the congruent and incongruent reaction times within
one condition was performed. As in Experiment 2, the
different-times condition showed a significant differ-
ence between the congruent and incongruent trials ($p <
0.02$; Figure 4c). The varying-prime condition did not
($p = 0.11$).

Error rates were analyzed by performing a two-way
repeated-measures ANOVA between the congruent
and incongruent error rates within each condition.
Again, the different-times condition showed significant
priming whereas the varying-prime condition did not
($p < 0.04$ and $p = 0.12$, respectively; Figure 4d).

Discussion

Experiment 3 confirms the results of the differ-
ent-offset condition of Experiment 2. When two vernier
primes with opposite offset direction are presented in
quick succession (ISI of 30 ms) at different locations,
Prime 2 dominates the response.

By varying the interprime interval while leaving the
SOA between Prime 1 and the target constant, we could
trace the time course of Prime 2’s dominance over
Prime 1 (varying-prime condition). The largest priming
effect occurs at an ISI of 150 ms (i.e., when the ISI is
long and the interprime interval is about 70 ms). When
the ISI grows shorter, the priming effect is reduced,
possibly by two mechanisms: first, because shorter ISIs
lead to smaller priming effects in the first place
(Vorberg et al., 2003), and secondly, because Prime 1
has increasingly more time to activate a response
opposite to Prime 2.

General discussion

Current models of response priming are based on the
idea of sequential accumulation of information from
primes and targets. The models assume that primes and
targets activate corresponding responses according to a
prespecified stimulus-response mapping (direct param-
er parameter specification; Klotz & Wolff, 1995; Kunde, Kiesel,
& Hoffmann, 2003; Neumann, 1990; Schmidt et al.,
2011). When the prime is congruent to the target, it
preactivates a correct response and thus speeds target
responses. When the prime is incongruent, however, it
preactivates the incorrect response. Preactivation de-

-ends on the ISI. When the target enters the
visuomotor system, activation of the primed response is
either continued (in congruent cases) or the target leads
to response accumulation in the opposite direction until
the effect of the prime is overridden. If the target fails
to countermand an incongruent prime, a response error
occurs. This type of model correctly predicts that
priming effects increase with ISI and errors occur
predominantly at long ISIs in incongruent trials
(Vorberg et al., 2003). Evidence for such models comes
also from the time courses of lateralized readiness
potentials (Dehaene et al., 1998; Eimer & Schlagheck-
Schmidt, 2007), primed pointing movements (Schmidt,
2002; Schmidt et al., 2006; Schmidt & Schmidt, 2009),
and stochastic simulations of diffusion models (Vor-
berg et al., 2003).

What happens in a situation with two sequential
primes? In independent-race models, accumulation of
information from the two primes occurs in independent
channels. These models predict that the first prime
dominates priming, which is clearly not the case in our
experiments.

Sequential accumulation models (e.g., the diffusion
model by Vorberg et al., 2003) predict that the second
prime dominates priming because it (a) has time to
counteract the effect of Prime 1 and (b) has time to
activate a response on its own. This is what we
observed in Experiments 2 and 3, in which the second
vernier prime dominated the priming effect. Particu-
larly, Experiment 3 shows that even when Prime 1
precedes Prime 2 by 100 ms, Prime 1 still fails to
dominate the response, providing, again, strong evi-
dence against an independent race model. However,
priming effects occurring that late in the response
activation process are difficult to explain even for
sequential accumulation models because such long
intervals allow for a long head start of Prime 1, which
should have led to dominance of that prime and even
provoked a response error.

Our results may be explained by a model in which
the primes and target enter a buffer stage in which they
integrate before the response is finally initiated and in
which recent information is favored over early infor-
mation. Such a time-selective buffer may be necessary
for explaining priming effects at very long ISIs, which
force participants to delay their responses because
otherwise they risk a high error rate due to ongoing
response accumulation by response-incongruent
primes. Hence, information persistence in a buffer stage
might explain why Prime 2 remains dominant even
when Prime 1 has a head start long enough to provoke
a high rate of response errors under conditions of
speeded instead of delayed responding. Such a two-
stage model was recently proposed for decision making
(Rüter, Marcille, Sprekeler, Gerstner, & Herzog, 2012;
Rüter, Sprekeler, Gerstner, & Herzog, 2013; Schar-
nowski, Hermens, Kammer, Öğmen, & Herzog, 2007)
and is supported by transcranial magnetic stimulation
experiments, which show that vernier fusion takes up to
400 ms (Rüter, Kammer, & Herzog, 2010; Scharnowski et al., 2009).

Our findings cannot be explained on a purely perceptual level. Both Experiments 2 and 3 show that sequential primes become integrated in the visuomotor system even if perceptual fusion is prevented by presenting them at different locations. Thus, integration can occur in the absence of fusion. This implies that integration is best viewed as a visuomotor process in which integration may occur at several levels ranging from early visual to late motor stages but definitely remains possible when early perceptual stages are ruled out. At the same time, the term fusion is best reserved for the special case in which integration results in an integrated conscious percept. This distinction is of theoretical importance: Although Experiments 2 and 3 clearly show that feature integration can occur in the absence of fusion, we can also speculate about the reverse possibility: fusion without integration. Studies in response priming have shown that priming effects can occur at very short delays between prime and target. For instance, Schmidt and colleagues (2006, experiment 2) reported an experiment in which a 17-ms color prime was presented at 0 ms, priming effects were, surprisingly, in the range of about 50 ms. This finding suggests that the visuomotor system is able to transmit sequential signals at high temporal resolution. Hence, there remains the fascinating possibility that fusion may occur in conscious perception without concomitant integration in the visuomotor system.

Keywords: priming, feature integration, feature fusion

Acknowledgments

We would like to thank Marc Repnow for technical help, Aaron Clark for help with programming, and Johannes Rüter for comments.

Commercial relationships: none.
Corresponding author: Julianne E. Grainger.
Email: Julianne.Grainger@gmail.com.
Address: Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique, Fédérale de Lausanne (EPFL), Switzerland.

References

Mattler, U. (2003). Priming of mental operations by