Short term plasticity of anticipatory postural adjustments in the button-triggered unloading task

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1 Introduction

We studied the acquisition of the anticipatory postural adjustment (APA) in a button-triggered self-unloading task. Subjects were asked to hold an object with one hand while the other hand pressed a button that caused the object to be lifted. Compared to cases where objects were lifted without internal supervision, the button-triggered self-unloading task produces an APA similar to, but smaller in magnitude than natural unloading, in which the subject's other hand removes the object from the hand holding it. The APA is defined as the reduction in upward acceleration in our self-unloading task relative to the upward acceleration in the external, unsupervised unloading task.

We examined whether the APA can be abolished in the short term by a catch trial, and whether this reduction in APA depends on the magnitude of the APA itself. We reasoned that a transient disturbance in the expected mapping between button press and object unloading should cause learned APAs to be transiently lowered, because the acquired APA for a catch trial in this novel task should be susceptible to the failure of the motor program. On the other hand, less-well-learned APAs should not be much affected by the catch trial, because they are hardly observed during the catch trial. Thus, well-learned APAs should be lowered after a catch trial, and their recovery times should depend on the frequency of catch trials and the strength of the APA.

2 Results

Figure 1 shows the averaged acceleration traces for a single subject for four types of trials. Note that the catch trial traces are almost identical. In general, late catch trials tend to have a more negative acceleration. The contrast between early and late normal trial accelerations are some what atypical in figure 1, because at time of unloading, late normal accelerations are actually larger than early normal accelerations. Usually, late normal accelerations tend to be smaller, indicative of the postural response learned during the course of the experiment. Note also that the window from about 0 to 100 milliseconds contains the rising phase of the unloading hand in response to the object being lifted away.

Figure 2 shows the mean accelerations over the 0 to 150 millisecond window for all trials, separated by subjects. Thus subject one's accelerations are found in the first segment, followed by subject two's, etc. Notice that in most of the subjects, there's a tendency for mean accelerations to decrease over the course of the trial. This indicates the acquisition of the APA. Note, however, that the rate at which the APA is acquired is different for each subject. The last subject, for example, does not acquire the APA as nearly as quickly as subject three. We'd expect the catch trial accelerations to be negative, because the same force is applied while the object is seen to be lifted away. Thus the catch trial acceleration indicates the net APA. In general, this value also decreases over time, but because the sample size is smaller, this decrease cannot be easily determined from the plot. Finally, we'd expect accelerations for trials right after the catch trials to be larger than normal, indicating a reduced APA. Again, there is some evidence of this, particularly in the quick-learning subjects such as subject 3. Figure 3 shows the same plot from figure 2 binned by every five trials, to smooth out the data. Here, the trial-after effect is more evident.

Table 1 shows the individual mean accelerations for each subject and each time of trial, broken down according to early (first 100 trials), middle (second 100 trials), and late (last 100 trials) periods. A paired samples t-test on the difference between late and early accelerations shows a significant difference from zero ($p < 0.025$), with a mean of -0.0641 for late minus early. This means the late average accelerations are significantly smaller than the early average accelerations across all subjects, which is indicative of acquisition of the APA. Comparisons across different trial types is more difficult to see, because of the number of different types (pre-catch, catch, catch+1, catch+2, etc.), so we'll examine that later.

Figure 4 shows the mean accelerations broken down by trial type, i.e. trial number relative to catch trial. The pre-catch trials have very similar means, as expected. Also as expected, the average acceleration for the late catch trials are more negative than the average acceleration for the early catch trials, compared by averaging over all subjects. This means the net APA is greater during the late trials. On the other hand, the post-catch responses are less clear. We had expected the early trial accelerations after catch trials to be roughly equal and large. Instead, we see a decrease in the mean accelerations over time after the catch trials during the early part of the experiment. Meanwhile, we'd expected the late trial accelerations to start off large right after the catch trial, then decline due to the learned APA. This is expected because only 10% of the trials are catch trials, so subjects should revert to their habitual APA responses in the latter part of the experiment. Instead, what we see is a constant mean acceleration very similar to pre-catch in the post-catch, indicating that the catch trial had no effect on the mean accelerations in subsequent trials. To deal with problems in which subjects lowered their arms before the object was unloaded, we calculated the percentage of trials in which the problem did not occur, which turns out to be almost always over 90%, as shown in figure 5. We then recomputed figure 4 based on only the good trials, as shown in figure 6. The basic pattern remains the same.

3 Discussions

Diedrichsen et al ([1]) found that a reduction in upward acceleration in the button-triggered unloading task compared to external unloading. This finding was used to justify the claim that a voluntary action was essential for acquiring an APA. In our study, we've confirmed the acquisition of the APA, and moreover, shown how it came about during the experiment through a process of learning. The basis for this learning was finding ([1]) that triggered unloading had smaller APAs than natural unloading. This indicates that the novel task was more difficult to time properly, and hence required a learning period. Although both triggered and natural unloading required a volitional action associated with the loading hand, only the natural unloading task affords direct physical contact between the two hands via the object as an intermediary. We've confirmed that we indeed see an APA in the triggered unloading task.

Diedrichsen et al ([2]) found that short-term plasticity in the triggered unloading task was impaired in patients with bilateral cerebellar damage. In our experiment, we observe limited short-term plasticity in the late trials after a catch trial, contrary to expectations. This may suggest that ipsilateral cerebellar involvement in the triggered unloading is reduced in well-learned trials with large APAs (i.e. small upward accelerations), although a rebound in the upward acceleration can still be seen (figure 4). However, subjects had also been repeating the task for a substantially amount of time when the late trials come up, so the lack of catch trials (10%) may cause them to go back to repeating a firmly-programmed motor procedure. When the motor program is well-entrenched in the latter parts of the experiment, the catch trial perturbations may be ignored by the cerebellum, and we get a reduction in short-term plasticity. If this were the case, we'd expect consecutive catch trials to produce a greater APA adaptation on trials thereafter.

We found significant acquisition of APA, as expected for normal subjects. However, we also found that adaptation of APA occurs relatively early (figure 4). This may indicate the cerebellum is more aware of discrepancies when learning a novel task. Hence, a catch trial causes the subsequent trial to have a large upward acceleration, essentially reverting back to external unloading, as the triggered unloading motor program breaks down. However, after 250 trials, the motor program has been practiced for over 200 times, and the cerebellum is immune to such discrepancies. According to this view, well-practiced unloading tasks should have small APA adaptation. Indeed, natural unloading should take place with little or no change in APA despite intervening tasks of little relevance. On the other hand, we predict that even more novel tasks should exhibit short-term plasticity in APA after disruption of the motor routine.

References

[1] J. Diedrichsen, T. Verstynen, A. Hon, S. L. Lehman, and R. B. Ivry. Anticipatory adjustments in the unloading task: Is an efference copy necessary for learning? *Experimental Brain Research*, 148:272–276, November 2003.

[2] J. Diedrichsen, T. Verstynen, S. L. Lehman, and R. B. Ivry. Cerebellar involvement in the integration of bimanual actions.

Figures

The next few pages contain the six figures and one table referenced. See also the files `Results_r5.xls`, which contains a plot similar to figure 4, but with the middle trials plotted as well.

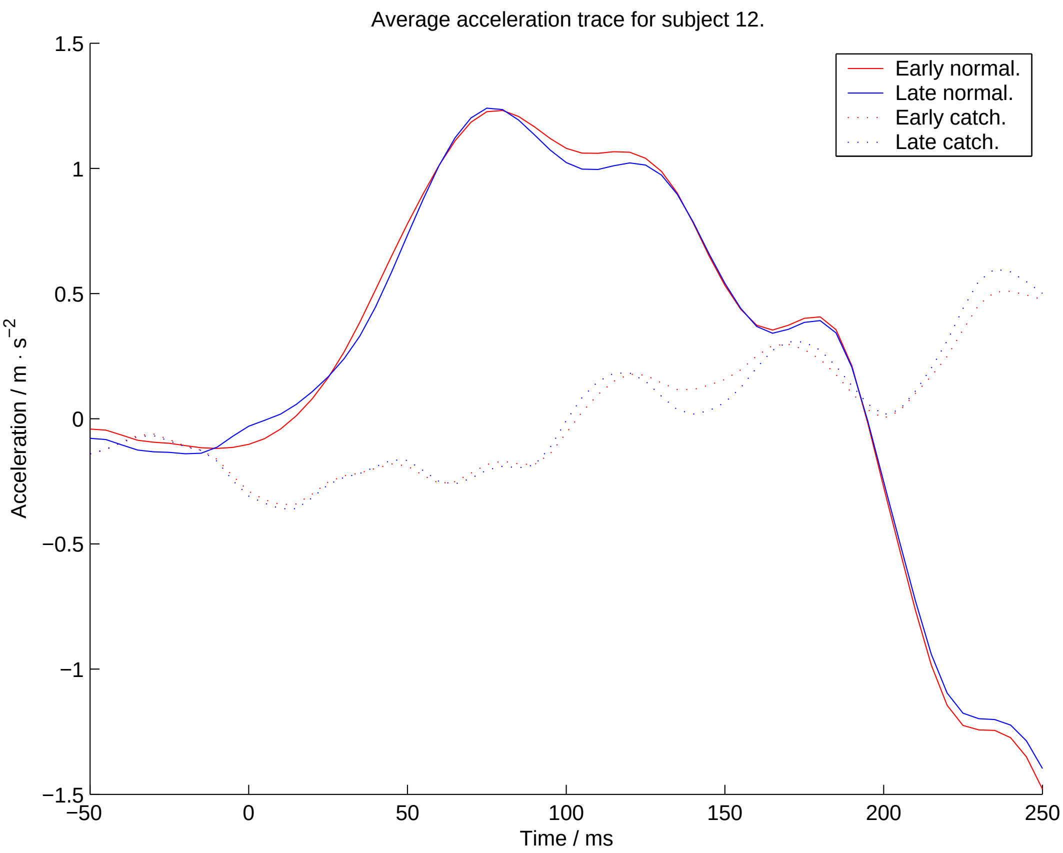

Figure 1: Acceleration trace averaged over early and late trials for the unloading hand of a representative subject. Zero time indicates time of unloading executed by the computer. Notice the lowered acceleration for the late trials compared to the early trials just before the unloading. This is usually indicative of the APA learned. However, if the subject releases the object before the unloading, the trial is counted as invalid.

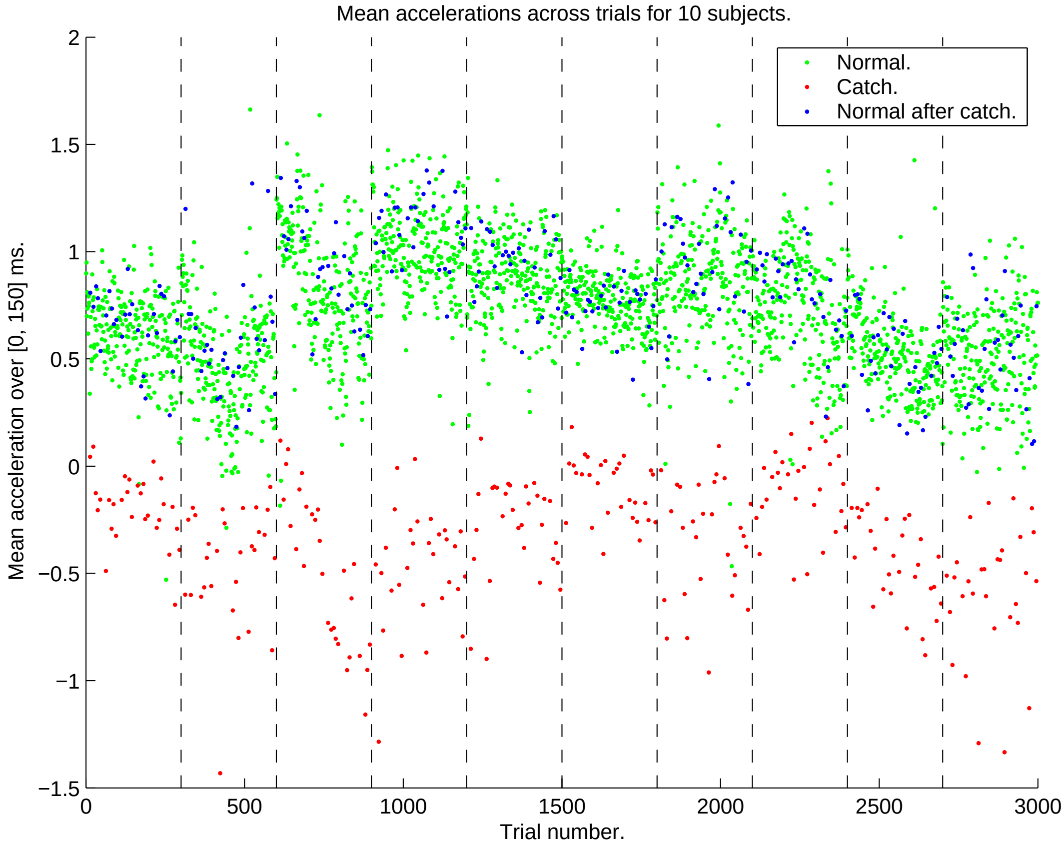

Figure 2: Mean accelerations for each trial of each subject, plotted together for comparison. Each block contains mean accelerations for each subject. The mean accelerations plotted within a block are ordered by the experimental coordinates (trial one, followed by trial two, etc. up to the last trial). Notice that the mean accelerations tend to decrease for each individual subject, indicating learning, but some subjects learn faster and better than others.

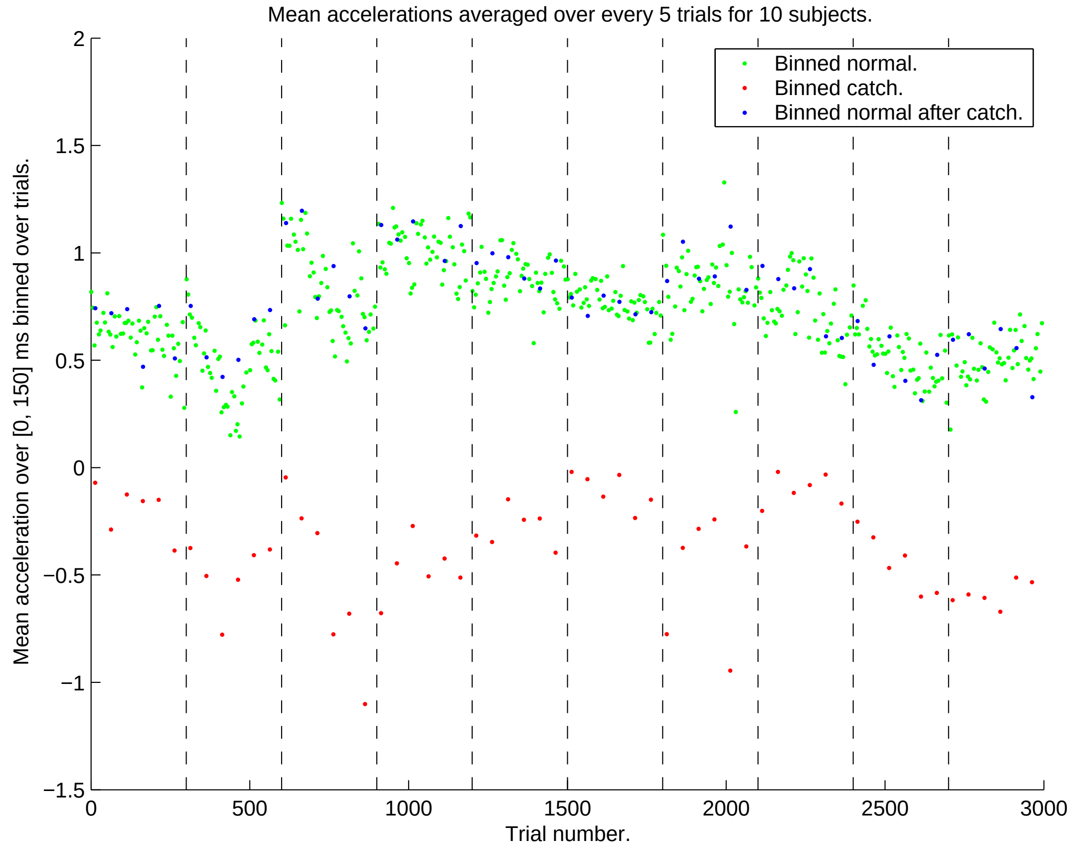

Figure 3: Same plot as figure 2, but binned by every five trials, to emphasize the direction of the change in mean accelerations. Notice that normal trials after catch trials tend to have high accelerations.

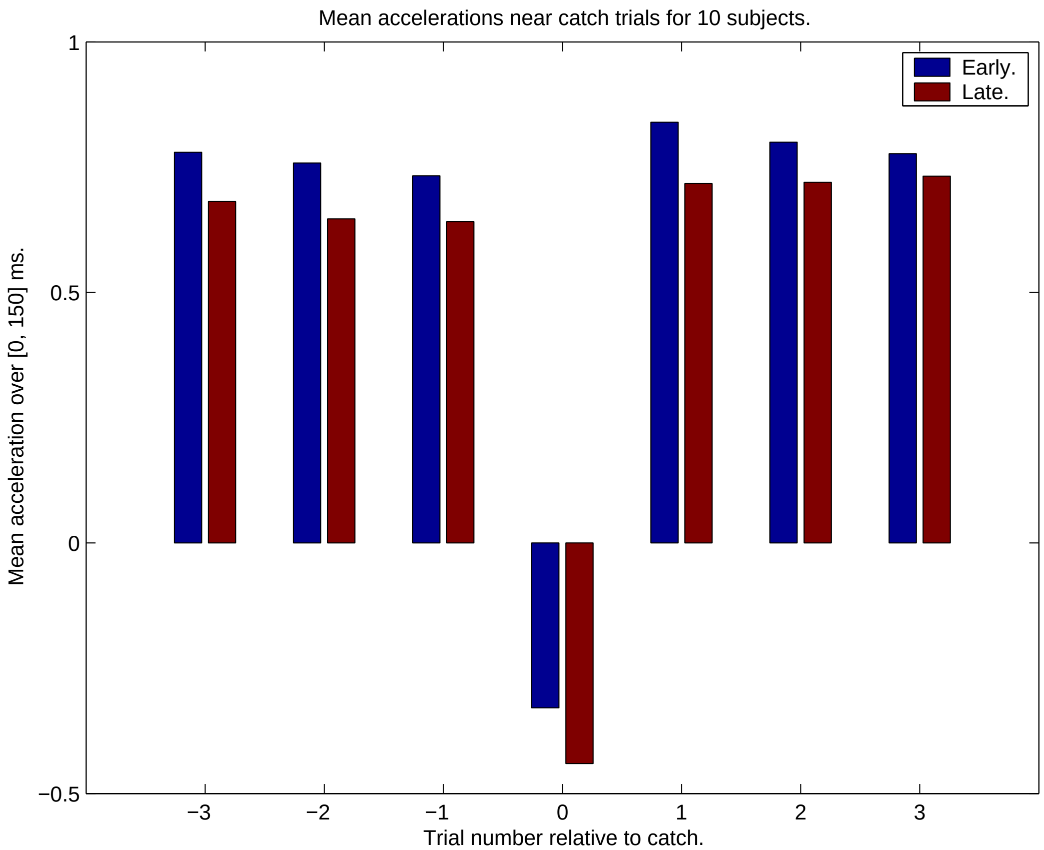

Figure 4: Average accelerations for trials before catch trials compared to average accelerations for trials after catch trials. Notice that mean accelerations go up after catch trials. Notice also that mean accelerations for late trials are smaller, indicating a larger APA. Moreover, the downward acceleration in catch trials are greater for late trials, again indicating a greater APA.

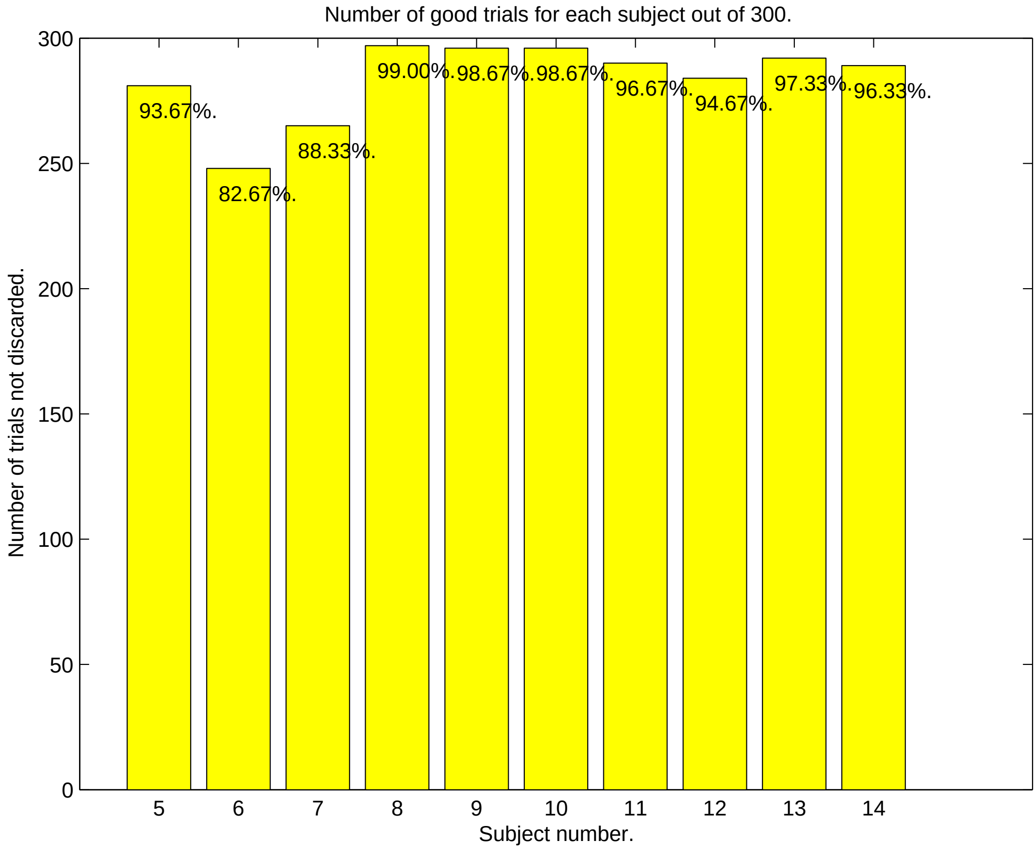

Figure 5: Percent of trials that were acceptable for each subject. Acceptable trials include those in which the subject did not pre-release the object prior to the unloading, and in which the subject did not fail to complete the trial.

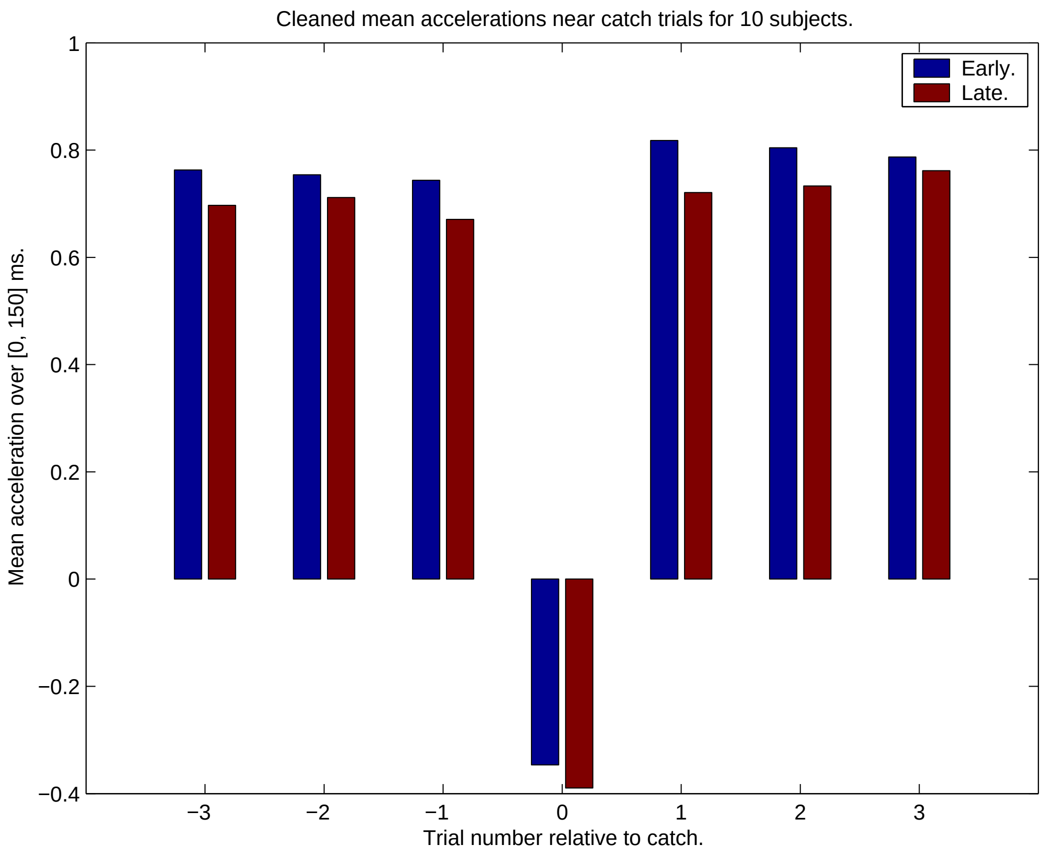

Figure 6: Same plot as figure 4, but with bad trials taken out. Notice that late trial accelerations are consistently lower, indicating a greater APA. However, after the catch trial, the late trial accelerations actually go up unexpectedly, while the early trial accelerations go down some what, contrary to the expected stabilization after catch.

Subject	Catch	Early	Middle	Late	Mean	Late-Early
5	-3	0.58	0.573	0.546	0.566	-0.034
5	-2	0.553	0.49	0.468	0.504	-0.085
5	-1	0.522	0.6	0.357	0.493	-0.165
5	0	-0.186	-0.176	-0.273	-0.212	-0.088
5	1	0.622	0.494	0.545	0.554	-0.077
5	2	0.602	0.495	0.528	0.542	-0.074
5	3	0.57	0.494	0.44	0.501	-0.13
6	-3	0.439	0.192	0.426	0.352	-0.013
6	-2	0.439	0.145	0.307	0.297	-0.131
6	-1	0.483	0.187	0.351	0.34	-0.132
6	0	-0.4	-0.671	-0.396	-0.489	0.004
6	1	0.524	0.384	0.61	0.506	0.086
6	2	0.478	0.34	0.512	0.443	0.034
6	3	0.375	0.302	0.417	0.365	0.043
7	-3	0.82	0.584	0.533	0.646	-0.287
7	-2	0.775	0.59	0.429	0.598	-0.346
7	-1	0.642	0.593	0.579	0.605	-0.063
7	0	-0.163	-0.573	-0.791	-0.509	-0.628
7	1	0.942	0.712	0.599	0.751	-0.343
7	2	0.759	0.625	0.639	0.674	-0.12
7	3	0.932	0.614	0.683	0.743	-0.249
8	-3	0.794	0.783	0.782	0.786	-0.012
8	-2	0.781	0.805	0.823	0.803	0.041
8	-1	0.72	0.796	0.818	0.778	0.097
8	0	-0.467	-0.351	-0.404	-0.407	0.063
8	1	0.875	0.978	0.854	0.902	-0.021
8	2	0.831	0.941	0.823	0.865	-0.008
8	3	0.836	0.834	0.836	0.835	0
9	-3	0.695	0.743	0.665	0.701	-0.029
9	-2	0.638	0.737	0.631	0.669	-0.007
9	-1	0.673	0.71	0.628	0.67	-0.045
9	0	-0.385	-0.197	-0.343	-0.308	0.042
9	1	0.766	0.737	0.72	0.741	-0.046
9	2	0.76	0.711	0.731	0.734	-0.029
9	3	0.741	0.71	0.749	0.733	0.008
10	-3	0.647	0.637	0.656	0.647	0.009
10	-2	0.751	0.675	0.671	0.699	-0.08
10	-1	0.656	0.604	0.654	0.638	-0.003
10	0	-0.023	-0.095	-0.124	-0.081	-0.101
10	1	0.626	0.67	0.633	0.643	0.007
10	2	0.685	0.664	0.628	0.659	-0.057
10	3	0.688	0.649	0.654	0.664	-0.034

Subject	Catch	Early	Middle	Late	Mean	Late-Early
11	-3	0.692	0.739	0.655	0.695	-0.037
11	-2	0.66	0.684	0.578	0.641	-0.082
11	-1	0.721	0.749	0.638	0.703	-0.082
11	0	-0.645	-0.249	-0.464	-0.453	0.181
11	1	0.764	0.743	0.829	0.779	0.065
11	2	0.74	0.806	0.685	0.744	-0.055
11	3	0.652	0.768	0.71	0.71	0.058
12	-3	0.531	0.633	0.502	0.555	-0.029
12	-2	0.569	0.611	0.477	0.552	-0.092
12	-1	0.6	0.652	0.396	0.549	-0.205
12	0	-0.155	-0.252	-0.227	-0.211	-0.072
12	1	0.767	0.726	0.536	0.676	-0.231
12	2	0.713	0.64	0.641	0.665	-0.071
12	3	0.655	0.77	0.637	0.687	-0.018
13	-3	0.518	0.385	0.37	0.424	-0.148
13	-2	0.536	0.433	0.447	0.472	-0.089
13	-1	0.487	0.36	0.307	0.385	-0.18
13	0	-0.233	-0.407	-0.556	-0.399	-0.323
13	1	0.492	0.434	0.336	0.421	-0.156
13	2	0.491	0.378	0.373	0.414	-0.119
13	3	0.492	0.408	0.411	0.437	-0.081
14	-3	0.54	0.359	0.578	0.492	0.038
14	-2	0.465	0.47	0.422	0.453	-0.043
14	-1	0.383	0.403	0.503	0.43	0.12
14	0	-0.521	-0.577	-0.428	-0.509	0.093
14	1	0.548	0.537	0.49	0.525	-0.058
14	2	0.503	0.475	0.533	0.504	0.03
14	3	0.443	0.452	0.545	0.48	0.102
Mean	-3	0.626	0.563	0.571	0.587	-0.054
	-2	0.617	0.564	0.525	0.569	-0.091
	-1	0.589	0.565	0.523	0.559	-0.066
	0	-0.318	-0.355	-0.401	-0.358	-0.083
	1	0.693	0.641	0.615	0.65	-0.077
	2	0.656	0.608	0.609	0.624	-0.047
	3	0.638	0.6	0.608	0.616	-0.03
	Mean	0.5	0.455	0.436	0.464	-0.064

Table 1: Table of mean accelerations broken down by subject, trial number relative to catch trials, and progress of experiment (early, middle, and late). Means are taken across experimental coordinates, then across trial numbers relative to catch. Notice that late trials usually have the lower accelerations, as do pre-catch trials, indicating larger APA.